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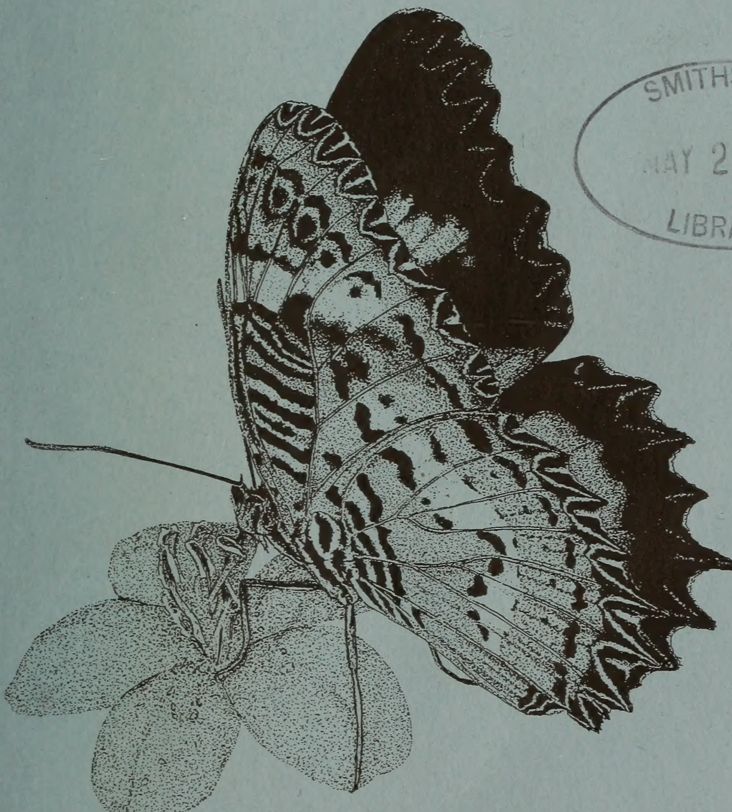

26 April 1996

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Cover illustration: The lacewing butterfly, *Cethosia biblis* (Nymphalidae), occurs in China and southeast Asia. Pen and ink drawing from photograph by Margarette Mead. Original drawing by Martie Clemons, Dudek & Associates Inc., 305 Third Street, Encinitas, California 92024.

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MONITORING THE FALL MIGRATION OF THE MONARCH BUTTERFLY *DANAUS PLEXIPPUS* L. (NYMPHALIDAE: DANAINAE) IN EASTERN NORTH AMERICA: 1991–1994

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ABSTRACT. The results of two different sampling methods are presented for summer resident and migrant monarch butterflies, *Danaus plexippus* L. (Nymphalidae: Danainae), in the northeastern region of North America during the period 1991–1994. Estimates of the relative numbers of butterflies obtained by the Xerces/NABA Fourth of July Butterfly Counts and by a newly instituted fall census in Cape May, New Jersey are correlated. Monitoring of the relative annual abundance of monarchs of the eastern population and its predicted decline therefore appears feasible. Our Cape May data, as well as historical records, indicate that the monarch's annual fall migration along the Atlantic Coast is a normal, and not an "aberrant" phenomenon. An alternative migration model, based on avian research, is presented as a possible adaptive explanation for the fall migratory movements of the monarch butterfly along the Atlantic Coast.

Additional key words: censusing, transect methods, Fourth of July Butterfly Counts, migration, Atlantic Coastal Plain, Cape May, New Jersey.

Monarch butterflies, *Danaus plexippus* L., remigrating from Mexico annually colonize large areas of North America east of the Rocky Mountains. Successive broods (Malcolm et al. 1993) move northward as far as southern Canada and the northeastern United States where multiple generations are produced each summer (Cockrell et al. 1993). During late summer and early fall, the year's final generation(s) of monarchs migrate southwestward (Urquhart 1960), with survivors ultimately reaching the overwintering sites in the Transverse Neovolcanic Belt of mountains in central Mexico (Urquhart 1976, Urquhart & Urquhart 1976, Brower 1977, 1985, Brower et al. 1977).

Although the monarch is a well studied organism, quantitative data

are lacking on its fall movements, including such basic factors as the phenology and the relative sizes of the migrations. Subsequent to the discovery of monarch overwintering sites in Mexico, a model for the autumnal movement of the eastern North American monarch population i.e., the population that breeds east of the Rocky Mountains, was proposed by Urquhart & Urquhart (1978, 1979) and Urquhart (1987). One aspect of this model dealt with the subset of monarchs found along the east coast—they maintained that migrants heading south along the Atlantic coast in the fall are largely wind drifted and off course. Urquhart described such migrants as "aberrant" and suggested that they ultimately end up in Bermuda or, via the Yucatan, in Central America (Urquhart 1987:138–143).

In reviewing monarch migration, Brower (1995) addressed the specific issues dealing with monarchs migrating to Bermuda, the Bahamas, and the Yucatan Peninsula and concluded that these are essentially "failures of the fall migration to Mexico." Citing the historical record as well as our studies at Cape May, Brower (1995) hypothesized that most migrants east of the Appalachians either move southwestward through the mountains, or follow the coast south to northern Florida, where they turn westward to follow the Gulf Coast on their way to the Mexican overwintering grounds.

Williams (1930) cited approximately 100 observations of migratory movements in North America, of which more than 25% refer to localities along the Atlantic Coast from Hampton, New Hampshire to Charleston, South Carolina (Williams 1930:141–149). These accounts extend back to the nineteenth century and indicate that southern New Jersey, and Cape May in particular, have long been known as concentration areas for southbound monarchs in the fall. For example, an account from Cape May stated "habitually seen according to Holland" (Williams 1930:149). Hamilton (1885) characterized the September 1885 monarch migration at Brigantine, New Jersey as "almost past belief . . . millions is but feebly expressive . . . miles of them is no exaggeration." Roger Tory Peterson (pers. comm.) recalled from his visits to Cape May in the early 1930s trees so completely covered with monarchs that they were "more orange than green." During the last quarter century, reports by hawk counters from the New Jersey Audubon Society's Cape May Bird Observatory have regularly mentioned substantial monarch flights (P. Dunne, pers. comm.). The collective force of these anecdotal accounts suggests that a fall migration of monarchs along the east coast is a normal, recurrent phenomenon.

The purpose of this paper is to present and evaluate a quantitative methodology for estimating the relative size of the monarch's annual fall migrations. We compare two sets of data obtained over four years, from

1991 through 1994. The first was obtained during the summer breeding seasons by the Xerces/NABA (North American Butterfly Association) Fourth of July Butterfly Counts (4JBCs). The second set of data was obtained during the fall migrations in Cape May, New Jersey using a procedure we developed and describe here.

Our results support the hypothesis that a migration along the Atlantic coast is part of the monarch's normal fall migration. More importantly, the estimates of the relative numbers of butterflies obtained by the two very different methods are significantly correlated. A long term study that combines these two independent estimates should therefore allow us to monitor the relative annual abundance of monarchs of the eastern population.

METHODS

The Fourth of July Butterfly Counts. The 4JBCs, initiated by the Xerces Society and now administrated by NABA, have been held annually since 1975. During the 1991–1994 seasons, the number of counts held throughout North America ranged from 145 to 249 (Opler & Swengel 1992, 1994, Swengel & Opler 1993, 1995). Each 4JBC covers a circular area with a diameter of 15 m (24 km). Participants conduct a one day census of all species of butterflies seen in their count area. The annual census reports include location, date, weather conditions, general habitat descriptions, land use, and notes on unique habitats as well as any significant changes in land use. Observational effort for each census is indicated by the number of observers, the number of field parties, total party hours, and total party miles. Relative abundance data can therefore be calculated as a function of the numbers of butterflies per species seen per party hour.

In her review of the "issues, problems, and opportunities" of the 4JBCs, Swengel (1990) enumerated a variety of potential pitfalls of using the data to analyze fluctuations in population sizes of various butterfly species. She concluded that the monarch, however, "is well-qualified for such a study because it is widespread, abundant, easily identified, and a habitat generalist" (Swengel 1990:398–399). In her original and subsequent analyses of monarch populations on both continent-wide and regional bases, Swengel (1994, 1996) used the mean numbers of monarchs per party hour from several of the counts to compare trends in various North American monarch populations.

We used the 4JBC database to extract the 1991–1994 monarch data for the summer breeding censuses made at the 68 sites listed in Table 1 and mapped in Fig. 1. Our data are thus a subset of the 4JBC censuses for the northeastern region, encompassing the area of the

TABLE 1. Fourth of July Butterfly Counts listed from north to south by latitude, and secondarily from east to west by longitude. Included are site names, site numbers (Ref), latitude and longitude coordinates (lat.N, long.W), census dates, the number of party hours (ph), the total number of monarchs seen (Dp), and the calculated values for monarchs per party hour (Dp/ph). The calculated means of all the censuses for each year are at the bottom of the table. Data extracted from Opler & Swengel (1992, 1994) and Swengel and Opler (1993, 1995).

				1991			
Location	Ref	lat.N	long.W	Date	ph	Dp	Dp/ph
Compton Co., QU	1	45.20	71.45	11/7	8.00	10	1.25
Parc Du Mont Oxford, QU	2	45.20	72.12	14/7	15.80	34	2.15
Missisiquoi, QU	3	45.08	72.48	—	—	—	—
North Hero, VT	4	44.55	73.09	21/6	5.25	2	0.38
Essex Co., VT	5	44.46	71.44	23/6	7.50	1	0.13
Colchester, VT	6	44.32	73.10	17/7	10.00	35	3.50
Camel's Hump, VT	7	44.26	72.51	1/7	9.00	5	0.56
LaPlatte Marsh, VT	8	44.24	73.14	28/7	4.00	9	2.25
Pinkham Notch, NH	9	44.16	71.15	—	—	—	—
Lake Placid, NY	10	44.15	73.59	—	—	—	—
Ferrisburg E., VT	11	44.13	73.15	14/7	4.00	24	6.00
Ferrisburg W., VT	12	44.13	73.15	15/7	3.00	39	13.00
Elizabethtown, NY	13	44.13	73.36	—	—	—	—
Hiram, ME	14	43.55	70.44	—	—	—	—
West Rutland, VT	15	43.35	73.09	—	—	—	—
Danby, VT	16	43.17	73.00	7/7	6.50	4	0.62
Saratoga Co. Arpt., NY	17	43.03	73.52	—	—	—	—
Antioch, NH	18	42.57	72.16	—	—	—	—
Vischer Ferry, NY	19	42.45	73.49	—	—	—	—
N. Berkshire Co., MA	20	42.37	73.07	—	—	—	—
C. Franklin Co., MA	21	42.34	72.31	17/7	32.50	184	5.66
Concord, MA	22	42.26	71.25	16/7	7.00	52	7.43
C. Berkshire Co., MA	23	42.24	73.15	—	—	—	—
S. Berkshire Co., MA	24	42.09	73.20	—	—	—	—
Lower Pioneer Vy., MA	25	42.08	72.33	21/7	5.20	0	0.00
Foxboro, MA	26	42.05	71.15	—	—	—	—
Salisbury, CT	27	42.00	73.21	—	—	—	—
Cumberland, RI	28	41.59	71.29	—	—	—	—
Sherman, CT	29	41.51	73.30	17/7	4.50	6	1.33
Storrs, CT	30	41.48	72.14	7/7	6.00	32	5.33
Bristol Co., MA	31	41.38	70.58	21/7	6.00	5	0.83
Rocky Hill, CT	32	41.38	72.39	—	—	—	—
Prudence Island, RI	33	41.37	71.18	—	—	—	—
Voluntown, CT	34	41.35	71.51	—	—	—	—
Stormville, NY	35	41.35	73.45	—	—	—	—
Monticello, NY	36	41.34	74.38	—	—	—	—
Aquidneck Island, RI	37	41.32	71.16	—	—	—	—
Meriden, CT	38	41.32	72.48	—	—	—	—
Great Swamp, RI	39	41.26	71.34	—	—	—	—
E. Fairfield Co., CT	40	41.19	73.12	—	—	—	—
E. Frfld./W. New Hav. Cos., CT	41	41.16	72.55	9/7	4.75	17	3.58
Fairfield Co., CT	42	41.12	73.18	27/7	1.00	1	1.00
N. Westchester Co., NY	43	41.12	73.41	14/7	44.00	230	5.23
Block Island, RI	44	41.10	71.33	—	—	—	—
Westport/Fairfield, CT	45	41.10	73.19	—	—	—	—
Springdale, NJ	46	41.05	74.49	—	—	—	—

TABLE 1. Extended.

1992				1993				1994			
Date	ph	Dp	Dp/ph	Date	ph	Dp	Dp/ph	Date	ph	Dp	Dp/ph
11/7	11.00	0	0.00	—	—	—	—	3/7	10.00	0	0.00
12/7	9.50	0	0.00	—	—	—	—	—	—	—	—
23/8	5.25	0	0.00	—	—	—	—	—	—	—	—
14/6	10.00	0	0.00	13/6	8.25	2	0.24	—	—	—	—
—	—	—	—	23/6	5.00	0	0.00	—	—	—	—
13/7	9.50	1	0.11	18/7	7.00	1	0.14	—	—	—	—
5/7	4.75	0	0.00	5/7	5.50	0	0.00	—	—	—	—
19/7	2.50	0	0.00	4/7	3.00	0	0.00	—	—	—	—
—	—	—	—	—	—	—	—	20/7	5.60	1	0.18
—	—	—	—	—	—	—	—	10/7	6.50	5	0.77
18/7	3.00	0	0.00	—	—	—	—	—	—	—	—
7/7	3.00	0	0.00	8/7	7.00	1	0.14	1/7	6.00	3	0.50
—	—	—	—	14/6	6.50	0	0.00	2/7	9.00	17	1.89
19/7	10.25	0	0.00	17/7	4.50	1	0.22	9/7	5.00	0	0.00
—	—	—	—	—	—	—	—	13/7	6.25	11	1.76
12/7	6.60	1	0.15	—	—	—	—	—	—	—	—
19/7	3.00	0	0.00	—	—	—	—	—	—	—	—
10/7	24.00	11	0.46	—	—	—	—	—	—	—	—
18/7	10.50	0	0.00	4/7	9.75	1	0.10	9/7	8.25	6	0.73
—	—	—	—	26/6	20.00	11	0.55	13/7	22.00	37	1.68
11/7	34.00	3	0.09	10/7	27.00	12	0.44	9/7	38.00	57	1.50
18/7	9.00	1	0.11	10/7	17.50	16	0.91	16/7	19.00	81	4.26
25/7	36.25	6	0.17	—	—	—	—	17/7	21.00	46	2.19
—	—	—	—	10/7	15.00	18	1.20	16/7	18.00	79	4.39
22/7	4.08	2	0.49	—	—	—	—	—	—	—	—
11/7	37.30	9	0.24	11/7	40.00	22	0.55	10/7	45.00	48	1.07
—	—	—	—	—	—	—	—	9/7	18.00	6	0.33
29/7	8.00	0	0.00	—	—	—	—	—	—	—	—
18/7	4.25	0	0.00	—	—	—	—	—	—	—	—
19/7	9.00	2	0.22	13/7	25.50	28	1.10	11/7	27.00	23	0.85
19/7	5.25	0	0.00	18/7	5.00	11	2.20	17/7	5.00	7	1.40
—	—	—	—	—	—	—	—	5/7	8.00	2	0.25
—	—	—	—	—	—	—	—	18/7	7.00	2	0.29
—	—	—	—	—	—	—	—	18/7	6.00	3	0.50
—	—	—	—	20/7	6.50	11	1.69	24/7	8.25	11	1.33
—	—	—	—	—	—	—	—	3/7	5.50	3	0.55
8/7	11.50	1	0.09	—	—	—	—	—	—	—	—
—	—	—	—	17/7	5.50	2	0.36	3/7	5.00	0	0.00
7/7	13.50	0	0.00	—	—	—	—	—	—	—	—
—	—	—	—	3/7	4.00	1	0.25	2/7	6.00	1	0.17
20/7	5.00	0	0.00	1/7	3.00	0	0.00	1/7	4.75	0	0.00
18/7	2.00	0	0.00	31/7	1.50	0	0.00	—	—	—	—
11/7	54.00	24	0.44	10/7	57.00	113	1.98	9/7	54.00	201	3.72
16/7	8.50	10	1.18	—	—	—	—	—	—	—	—
—	—	—	—	17/7	2.50	10	4.00	—	—	—	—
5/7	31.00	2	0.06	11/7	32.00	18	0.56	9/7	24.50	27	1.10

TABLE 1. Continued.

Location	Ref	lat.N	long.W	1991 Date	ph	Dp	Dp/ph
West Milford, NJ	47	41.05	74.22	28/7	8.00	9	1.13
Long Pond, PA	48	41.03	75.27	—	—	—	—
Greenbrook Sanc., NJ	49	40.54	73.56	20/7	7.00	2	0.29
Brooklyn/Queens Cos., NY	50	40.52	73.54	6/7	24.00	246	10.25
Muttontown, NY	51	40.51	73.32	20/7	33.00	106	3.21
Great Swamp, NJ	52	40.47	74.28	—	—	—	—
Bronx/Manhattan Co., NY	53	40.41	73.51	29/6	27.00	21	0.78
Mariton Wildl. Sanc., PA	54	40.41	75.19	15/6	5.00	2	0.40
Western Suffolk, NY	55	40.40	73.45	30/7	32.00	60	1.88
Staten Island, NY	56	40.35	74.09	22/6	25.00	18	0.72
Hawk Mountain, PA	57	40.35	75.55	—	—	—	—
Pool Wildl. Sanc., PA	58	40.33	75.31	15/6	1.50	0	0.00
Raritan Canal, NJ	59	40.25	74.34	11/7	28.00	126	4.50
Hendricks, PA	60	40.20	75.15	10/8	3.50	14	4.00
Furnace Hills, PA	61	40.13	76.18	—	—	—	—
S. Bucks Co., PA	62	40.11	74.54	—	—	—	—
Bryn Mawr, PA	63	40.02	75.19	15/7	15.00	74	4.93
White Clay Ck., PA	64	39.42	75.45	11/7	5.00	29	5.80
Galloway Township, NJ	65	39.29	74.34	7/7	4.00	9	2.25
Cumberland Co., NJ	66	39.20	75.12	15/6	6.00	34	5.67
Belleplain, NJ	67	39.15	74.56	14/7	32.50	105	3.23
Cape May, NJ	68	39.01	74.52	6/7	37.50	68	1.81
No. Sites and Mean Dp/h				**n = 36**			**3.09**

northern Appalachian Mountains and eastward, including southeastern Quebec, eastern New York and Pennsylvania east to the Atlantic coast, and thence southward through New England to southern New Jersey. Note that site 68 is Cape May, New Jersey where the fall censuses also were made. Table 1 presents the data for the 1991–1994 censuses.

The Cape May Census. Sutton et al. (1991) estimated that 10,106 monarchs passed their lookout at East Point, New Jersey during September through November 1990, with peak flights occurring on 28 September (1,500 monarchs) and 6 October (1,000 monarchs). On 27 September 1990, Walton recorded 618 monarchs moving southwest along the dunes at Cape May Point State Park in one 8-minute period. The following day at the same location the flight averaged 536 monarchs per hour between 0832 h and 1541 h (EST). These informal observations confirmed Cape May Point as having excellent potential for annual monitoring.

Systematic quantitative data collection was initiated at Cape May Point (hereafter called Cape May) during September-October 1991 by Walton and colleagues, under the aegis of the Monarch Migration Association of North America (c/o 7 Concord Greene No. 8, Concord,

TABLE 1. Extended continued.

1992				1993				1994			
Date	ph	Dp	Dp/ph	Date	ph	Dp	Dp/ph	Date	ph	Dp	Dp/ph
19/7	5.00	1	0.20	27/6	10.00	0	0.00	26/6	16.50	4	0.24
—	—	—	—	—	—	—	—	11/7	6.50	5	0.77
18/7	6.00	0	0.00	17/7	6.00	0	0.00	16/7	6.50	3	0.46
3/7	32.00	3	0.09	5/7	16.00	39	2.44	—	—	—	—
18/7	34.00	50	1.47	17/7	36.00	173	4.81	16/7	37.00	135	3.65
—	—	—	—	—	—	—	—	2/7	26.00	9	0.35
17/6	26.00	1	0.04	26/6	43.00	5	0.12	26/6	22.00	0	0.00
20/6	2.00	0	0.00	23/6	1.50	2	1.33	25/6	1.50	0	0.00
28/6	45.00	0	0.00	3/7	43.00	11	0.26	2/7	52.00	17	0.33
21/7	5.00	0	0.00	18/7	8.00	16	2.00	26/6	8.75	9	1.03
11/7	15.00	0	0.00	3/7	9.50	1	0.11	9/7	17.50	12	0.69
13/6	1.50	0	0.00	19/6	2.00	0	0.00	18/6	2.00	0	0.00
8/7	22.25	0	0.00	15/7	21.25	32	1.51	11/7	18.50	18	0.97
12/8	2.50	0	0.00	—	—	—	—	—	—	—	—
—	—	—	—	26/7	9.25	3	0.32	4/7	9.80	8	0.82
—	—	—	—	26/6	4.00	0	0.00	16/7	9.50	9	0.95
13/7	12.00	0	0.00	28/6	5.00	9	1.80	5/7	6.25	1	0.16
10/7	4.75	0	0.00	—	—	—	—	1/7	6.50	1	0.15
14/7	5.50	4	0.73	18/7	3.50	8	2.29	5/7	5.33	16	3.00
5/7	29.00	6	0.21	27/6	29.00	39	1.34	9/7	28.00	48	1.71
4/7	31.50	3	0.10	26/6	38.00	24	0.63	8/7	33.00	33	1.00
28/6	21.50	4	0.19	18/6	23.00	17	0.74	25/6	38.00	22	0.58
	n = 48		**0.14**		**n = 42**		**0.87**		**n = 47**		**1.03**

Massachusetts 01742, USA); the censusing was continued in the falls of 1992–1994. Based on methods developed by Pollard (1977), data were collected along a census route through a variety of habitats, including southern hardwood forest, agricultural fields, brackish wetland meadow, suburban neighborhoods, and coastal dunes along the Atlantic Ocean and Delaware Bay. While the 1992–1994 route covered a single 8 km transect, the 1991 census employed three shorter transects, albeit of approximately the same total distance and over much of the same ground covered in 1992–1994 (Fig. 2).

Each transect census was made by a single observer driving a car at approximately 32–40 km per hour, with all monarchs counted along the route. No stops were allowed to count specific concentrations of butterflies. Monarch totals, starting and elapsed times, and local weather conditions were recorded during each census. These census data are summarized in Table 2.

Statistical analyses. We used Statview II, version 1.03 (Feldman et al. 1987) to run regression analyses that relate the four annual averages of monarchs seen per census hour at Cape May to the average number of monarchs seen per party hour in the four 4JBC censuses. In these regressions, we defined the Cape May data as the dependent variable,

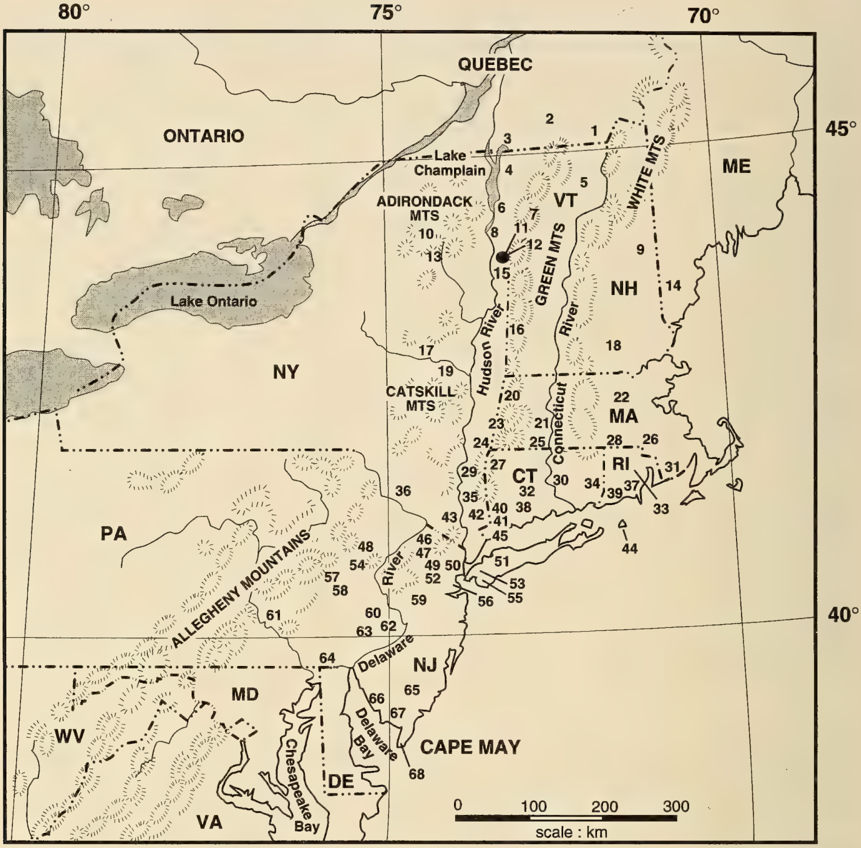

FIG. 1. Geographic distribution of 68 monarch butterfly census locations of the Fourth of July Butterfly Counts in the northeastern USA, made during the summers of 1991 through 1994. Site 68 is the location of the Cape May road census. See Table 1 for exact locations and yearly census data.

on the rationale that the number of migrants is dependent upon the size of the summer breeding populations.

RESULTS

Table 1 summarizes the 1991–1994 4JBC data for the Northeast in the area from the Appalachian mountain region east through the coastal

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FIG. 2. Cape May, New Jersey, showing the census routes over the four years. The 8 km route used in 1992–1994 is indicated by arrows. The crosses at the west end of Sunset Boulevard indicate the end of the truncated transect segment traversed in 1991. The base map is reproduced with the permission of P. Sutton of The Cape May Bird Observatory.

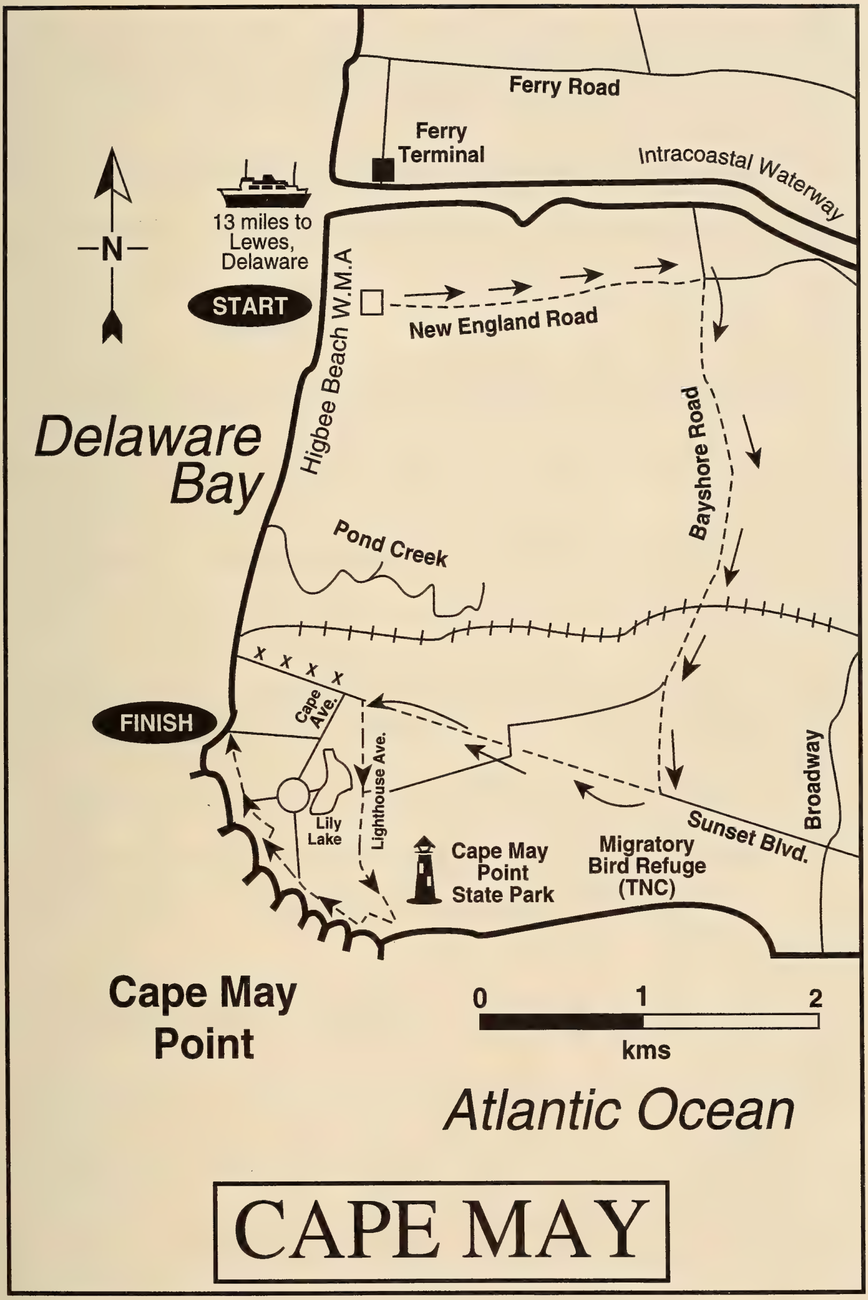
Ferry Road
Ferry Terminal
Intracoastal Waterway
13 miles to Lewes, Delaware
N
START
Higbee Beach W.M.A
New England Road
Delaware Bay
Bayshore Road
Pond Creek
FINISH
Cape Ave.
Lighthouse Ave.
Lily Lake
Cape May Point State Park
Migratory Bird Refuge (TNC)
Sunset Blvd.
Broadway
Cape May Point
0
1
2
kms
Atlantic Ocean
CAPE MAY

TABLE 2. Summary of the 1991-94 Cape May, New Jersey fall monarch migration census data. Included are the census dates, the number of census runs (cr), the total minutes of observation (min), the number of monarchs observed (Dp), and the calculated values for the average number of monarchs seen per census hour per day (Dp/h). The calculated means for the number of monarchs per census hour for each year are at the bottom of the table.

	1991				1992				1993				1994			
Date	cr	min	Dp	Dp/h	cr	min	Dp	Dp/h	cr	min	Dp	Dp/h	cr	min	Dp	Dp/h
1 Sep	—	—	—	—	3	61	16	15.74	3	46	12	15.65	3	52	48	55.38
2 Sep	—	—	—	—	3	56	11	11.79	3	48	9	11.25	3	52	58	66.92
3 Sep	—	—	—	—	3	50	6	7.20	3	48	3	3.75	3	50	19	22.80
4 Sep	—	—	—	—	3	59	9	9.15	3	46	1	1.30	3	51	20	23.53
5 Sep	—	—	—	—	3	58	2	2.07	3	45	13	17.33	3	50	58	69.60
6 Sep	—	—	—	—	3	55	0	0.00	3	48	19	23.75	3	53	229	259.25
7 Sep	—	—	—	—	3	54	6	6.67	3	51	9	10.59	3	52	151	174.23
8 Sep	—	—	—	—	3	58	6	6.21	3	46	8	10.43	3	53	162	183.40
9 Sep	—	—	—	—	3	51	2	2.35	3	17	1	3.53	3	52	119	137.31
10 Sep	—	—	—	—	3	55	6	6.55	3	48	6	7.50	3	52	163	188.08
11 Sep	—	—	—	—	3	62	10	9.68	3	50	13	15.60	3	50	187	224.40
12 Sep	—	—	—	—	3	62	37	35.81	3	59	26	26.44	3	52	200	230.77
13 Sep	—	—	—	—	3	60	23	23.00	3	61	16	15.74	3	53	287	324.91
14 Sep	1	5	14	168.00	3	60	17	17.00	3	63	9	8.57	3	52	185	213.46
15 Sep	1	5	8	96.00	3	53	7	7.92	3	55	17	18.55	3	50	46	55.20
16 Sep	1	5	5	60.00	3	61	7	6.89	3	58	52	53.79	3	50	3	3.60
17 Sep	—	—	—	—	3	55	4	4.36	3	58	79	81.72	3	52	1	1.15
18 Sep	1	5	12	144.00	3	55	5	5.45	3	38	47	74.21	3	55	140	152.73
19 Sep	4	30	34	68.00	3	53	44	49.81	3	61	299	294.10	3	55	456	497.45
20 Sep	2	15	98	392.00	3	54	16	17.78	3	59	153	155.59	3	57	44	46.32
21 Sep	3	20	131	393.00	3	51	8	9.41	1	19	8	25.26	3	55	76	82.91
22 Sep	1	10	109	654.00	3	50	2	2.40	3	57	198	208.42	—	—	—	—
23 Sep	1	10	2	12.00	3	54	21	23.33	3	56	150	160.71	1	18	6	20.00
24 Sep	2	15	46	184.00	3	55	8	8.73	3	53	237	268.30	3	54	75	83.33
25 Sep	—	—	—	—	—	—	—	—	3	54	176	195.56	3	57	27	28.42
26 Sep	1	10	0	0.00	3	56	28	30.00	3	54	71	78.89	—	—	—	—
27 Sep	2	10	3	18.00	3	57	3	3.16	3	34	6	10.59	3	55	11	12.00
28 Sep	2	10	10	60.00	3	53	24	27.17	3	54	92	102.22	3	55	51	55.64
29 Sep	3	20	15	45.00	3	48	1	1.25	3	55	267	291.27	2	35	11	18.86
30 Sep	2	20	18	54.00	3	51	10	11.76	1	19	52	164.21	3	55	203	221.45

TABLE 2. Continued.

Date	1991 cr	1991 min	1991 Dp	1991 Dp/h	1992 cr	1992 min	1992 Dp	1992 Dp/h	1993 cr	1993 min	1993 Dp	1993 Dp/h	1994 cr	1994 min	1994 Dp	1994 Dp/h
1 Oct	4	30	5	10.00	3	47	6	7.66	3	51	93	109.41	3	55	222	242.18
2 Oct	1	10	3	18.00	3	47	10	12.77	1	17	17	60.00	3	55	404	440.73
3 Oct	3	20	10	30.00	3	68	12	10.59	2	37	48	77.84	3	56	69	73.93
4 Oct	3	27	11	24.44	3	58	6	6.21	3	54	205	227.78	3	51	20	23.53
5 Oct	5	40	19	28.50	3	54	4	4.44	3	54	37	41.11	2	32	6	11.25
6 Oct	5	40	34	51.00	3	58	4	4.14	3	49	37	45.31	3	46	4	5.22
7 Oct	3	30	96	192.00	3	55	3	3.27	3	50	29	34.80	3	48	11	13.75
8 Oct	5	40	226	339.00	3	58	7	7.24	3	47	67	85.53	3	49	15	18.37
9 Oct	5	40	201	301.50	3	54	2	2.22	3	49	43	52.65	2	35	5	8.57
10 Oct	3	20	22	66.00	3	59	26	26.44	1	17	52	183.53	3	45	3	4.00
11 Oct	4	30	470	940.00	3	54	14	15.56	3	51	27	31.76	3	50	29	34.80
12 Oct	1	10	52	312.00	3	58	38	39.31	—	—	—	—	3	50	21	25.20
13 Oct	—	—	—	—	3	63	55	52.38	2	33	7	12.73	3	47	1	1.28
14 Oct	—	—	—	—	3	61	20	19.67	3	50	11	13.20	2	31	1	1.94
15 Oct	3	20	24	72.00	2	29	9	18.62	3	51	20	23.53	2	31	0	0.00
16 Oct	3	20	8	24.00	2	28	3	6.43	2	35	26	44.57	2	34	19	33.53
17 Oct	—	—	—	—	2	29	4	8.28	1	16	3	11.25	2	33	17	30.91
18 Oct	3	20	25	75.00	2	34	0	0.00	2	32	14	26.25	2	30	6	12.00
19 Oct	3	20	30	90.00	1	14	0	0.00	2	33	5	9.09	2	32	25	46.88
20 Oct	—	—	—	—	2	25	0	0.00	—	—	—	—	2	33	18	32.73
21 Oct	3	20	8	24.00	2	30	0	0.00	2	36	6	10.00	2	33	32	58.18
22 Oct	3	20	2	6.00	2	30	0	0.00	2	34	1	1.76	2	31	10	19.35
23 Oct	3	20	2	6.00	2	28	2	4.29	2	33	7	12.73	—	—	—	—
24 Oct	3	20	6	18.00	2	26	0	0.00	2	32	8	15.00	2	33	42	76.36
25 Oct	—	—	—	—	2	29	1	2.07	2	35	20	34.29	2	33	48	87.27
26 Oct	—	—	—	—	2	28	0	0.00	1	17	5	17.65	—	—	—	—
27 Oct	—	—	—	—	2	28	0	0.00	1	17	6	21.18	2	31	12	23.23
28 Oct	—	—	—	—	2	19	0	0.00	2	32	5	9.38	2	31	12	23.23
29 Oct	—	—	—	—	2	26	0	0.00	2	32	9	16.88	2	31	8	15.48
30 Oct	—	—	—	—	2	30	0	0.00	—	—	—	—	2	30	7	14.00
Mean				**142.20**				**10.40**				**62.90**				**86.30**

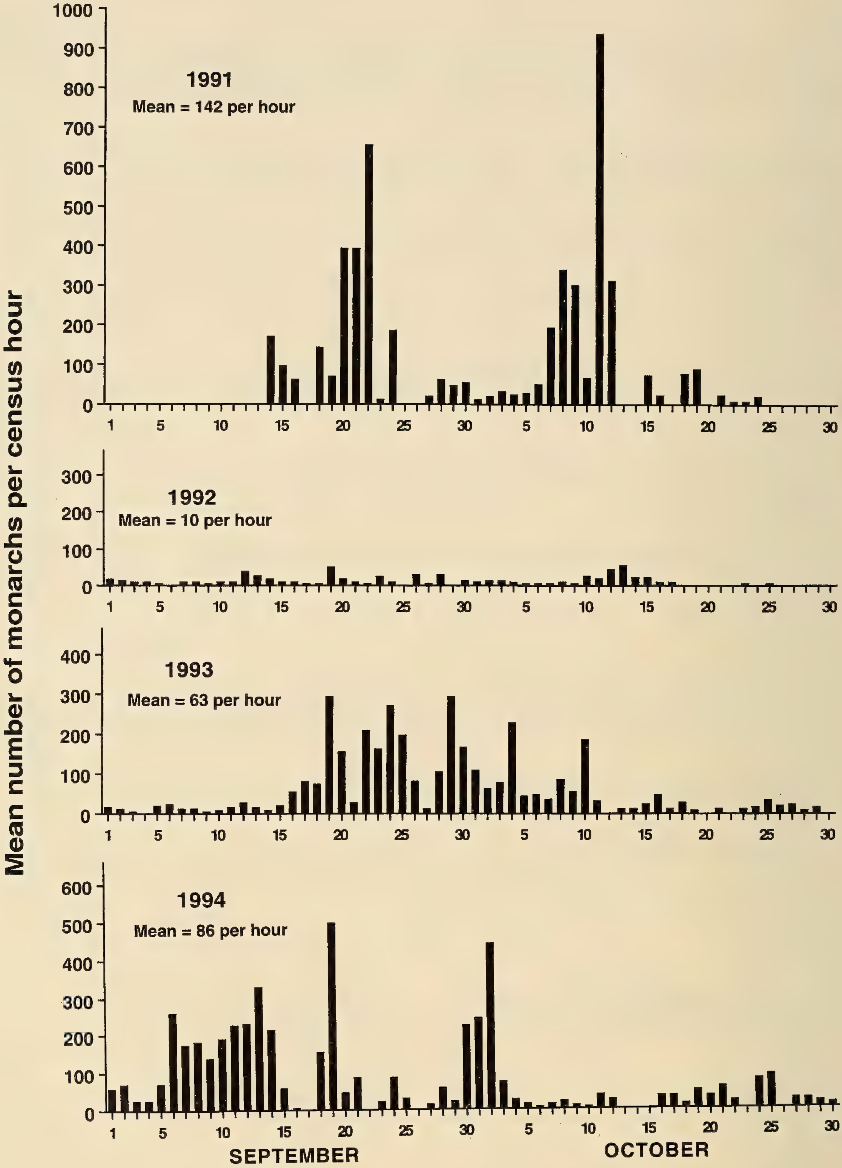

FIG. 3. The daily migration pattern of monarchs along the Atlantic Coast at Cape May, New Jersey during the 1991–1994 fall migrations, based on data in Table 2. Note that: (a) the migration extends over a period of approximately 8 weeks during September and October; (b) there is a greater than fourteen-fold difference in size between the minimum (1992) and maximum (1991) migrations; and (c) there appears to be more than a single pulse of migrant butterflies, which may represent migrants of successive generations (see also Fig. 4). In 1991, no counts were made on 1–13, 17 and 25 September, and on 13, 14, 17, 20, and 25–30 October. Zeros on the 1992–1994 graphs include both

plain. A total of 36 sites reported in 1991, 48 in 1992, 42 in 1993, and 47 in 1994 (Table 1). The calculated figures for the mean numbers of monarchs seen per party hour were: 3.09 for 1991, 0.14 for 1992, 0.87 for 1993, and 1.03 for 1994.

Table 2 summarizes the daily census results at Cape May, New Jersey. During the 1991 season, 93 census runs were conducted between 14 September to 24 October and a total of 1,759 monarchs was counted in 11.5 hours of observation. During the 1992 season, 160 census runs were conducted between 1 September to 30 October and a total of 565 monarchs was counted in 47.2 hours of observation. During the 1993 season, 145 census runs were conducted between 1 September to 30 October and a total of 2,857 monarchs was counted in 40.9 hours of observation. During the 1994 season, 148 census runs were conducted between 1 September to 30 October, and a total of 4,103 monarchs was counted in 42.1 hours of observation. The mean numbers of monarchs per party hour were 142.2 for 1991, 10.4 for 1992, 62.9 for 1993, and 86.3 for 1994.

Figure 3 presents histograms of the daily numbers of monarchs per census hour for each year at Cape May. Because so few monarchs migrated in 1992, Figure 4 shows the same 1992 data on an expanded scale. Figure 5 is a plot of the four seasonal averages obtained by the Cape May censuses (y axis) against the 4JBC censuses (x axis). The regression ($y = 41x + 23$) indicates that the data for the two censuses are significantly correlated ($r^2=0.905$, $F=19.0$, $p=0.049$). We also ran an additional regression that included a hypothetical 0:0 pair of values to the four years' data. It is not unreasonable to do this, because if there were no breeding in the northeastern area, it is likely that there would be virtually no migration through Cape May. This regression ($y = 45x + 14$) was also significant ($r^2=0.913$, $F=31.4$, $p=0.011$).

DISCUSSION

Correlation of the 4JBCs and the Cape May counts. The Fourth of July Butterfly Counts and the Cape May, New Jersey censuses are very different measures of monarch populations in the northeastern region of North America. Besides the methodological differences, the 4JBCs are a measure of the relative size of the summer breeding population, while the Cape May transects are a measure of the migrating population in the fall i.e., the two record different parts of the monarchs'

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rain days when no censuses were made and days when no monarchs were observed (see Table 2).

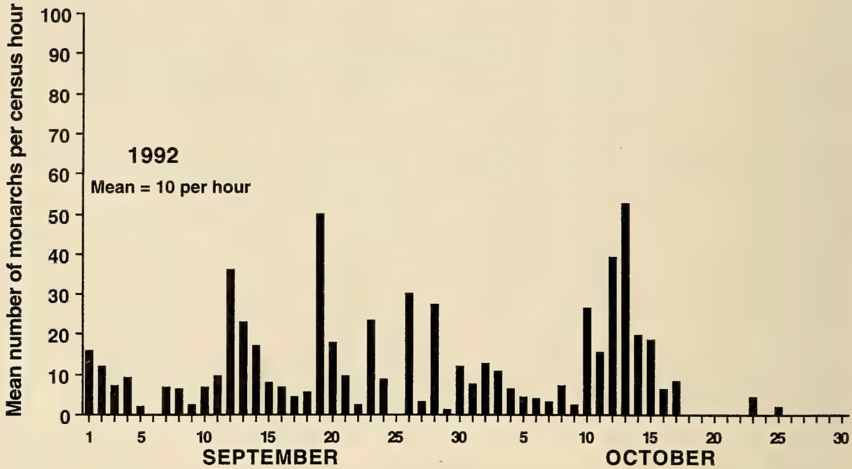

FIG. 4. The same Cape May, New Jersey data for 1992 as shown in Fig. 3, but scaled up to clarify the phenology of the migration.

annual cycle. We had originally thought that a correlation between the two would at best be weak because of the 4JBC methodologies (Swengel 1990). However, the implication of the significant correlation is that the size of the fall migration along the Atlantic coast can be predicted from the magnitude of the summer breeding population in the northeastern United States. Although more years are needed to confirm this relationship, the data suggest that the 4JBCs and the Cape May census procedures are both valid techniques for estimating the relative size of the monarch population from the Appalachians eastwards.

While our major goal for the Cape May census is to compile at least a ten-year data base, the results of the first 4 years include several additional findings of interest. Of particular note is the major decline in 1992 detected by both measures. This decline corresponds with observations of severe mortality in the Transverse Neovolcanic Belt overwintering sites in Mexico during the preceding winter i.e., in February 1992 (Brower *in* Culotta 1992). Swengel's (1993) summary of all 4JBC data for monarchs east of the Rocky Mountains for 1980–1993 indicated that the summer of 1992 was an average year. Compared to 1991, however, the numbers in the midwestern states were down about 65% in the summer of 1992. If only the northeastern 4JBCs sites are considered (i.e., those in Table 1), the decline from 1991 to 1992 was 95% (= {3.09–0.14/3.09}). This drop closely agrees with our Cape May data, which showed a 93% decline (= {142.16–10.41/142.16}).

Data from both counts in future years should thus continue to provide an annual measure of the regional fluctuations in monarch numbers

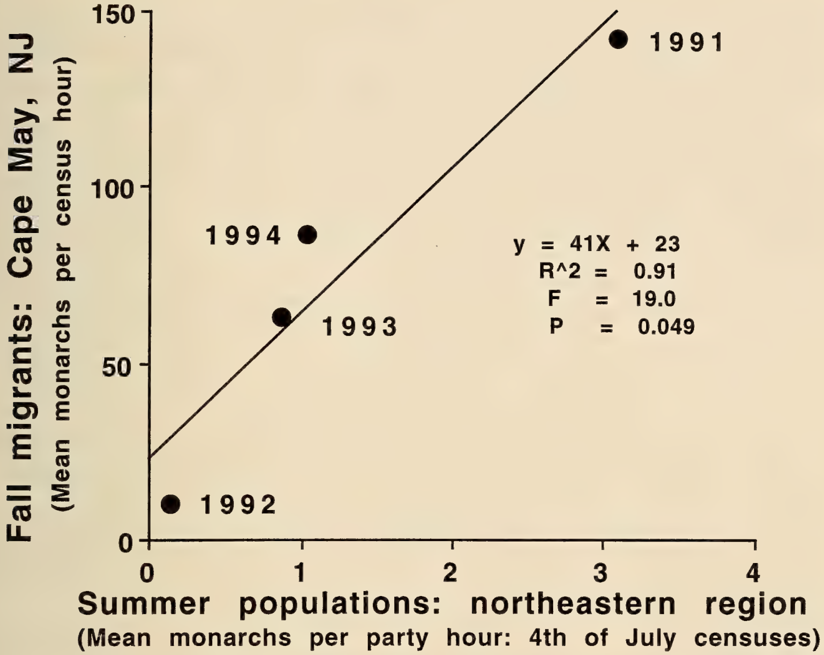

FIG. 5. Relationship of the yearly means of the 1991–1994 transect censuses made during the fall migration at Cape May, New Jersey and the mean Fourth of July Butterfly Counts made during the summer breeding season for the same four years in the northeastern USA. The Fourth of July Butterfly Count data are from the sampling sites in Fig. 1 and Table 1. The Cape May data are the yearly means of the annual fall migrant census counts from Table 2. The two estimates, made during different seasons and using different methods, are correlated ($r^2=0.91$) and the regression of the Cape May data on the 4JBC data is statistically significant ($F=19.0$, $p<0.05$). The correlation is evidence that both methods are valid estimates of the relative annual abundance of monarchs in the northeastern region, and that the 4JBC estimate of the summer breeding population in the northeast is a good predictor of the relative size of the fall migrant population along the Atlantic coast.

east of the Appalachians, as well as furnishing data for comparison with other regions of the country.

The Atlantic coast migration is not aberrant. During the four-year period of our study we have consistently recorded large numbers of monarchs at Cape May, New Jersey, ranging from 565 to 4,103 individuals (Table 2). We have also regularly observed migratory behaviors including: (1) mass movements along beach and dune lines; (2) a high degree of directionality of monarchs observed both during point counts and during counts of the butterflies crossing Delaware Bay (Walton et al., unpubl. data); (3) roost formations; and (4) significant build-ups and exoduses on consecutive days. Another notable characteristic has been

the timing of the fall movement. In each of the four years studied, the numbers of migrants peaked during the third week of September (Figs. 3–4). A second annual peak also is apparent in 1991, 1992, and 1994.

Our Cape May observations argue in favor of describing the Atlantic coast migrants as routine constituents in the monarch's fall migration. The numbers and behavior of monarchs observed leave little doubt that a significant migration has occurred at Cape May in each year of our censuses. Aspects of the timing of the migration, in particular the recurring September peaks, also indicate a routine passage of monarchs. Such consistent timing of the peaks would be unlikely if they were caused solely by weather conditions such as cold fronts, because the latter do not occur at the same time each year. Finally, the correspondence of the Cape May and 4JBC data sets suggests that the number of monarchs passing through Cape May is representative of northeastern breeding populations as a whole. If this correlation holds in future years, it will strengthen the hypothesis that the Cape May migration is representative of the population of northeastern monarchs, rather than comprising an "aberrant" group displaced by atypical weather conditions, as hypothesized by the Urquharts.

It is instructive to examine briefly the data and inferences that underlie the Urquharts' position. Maps based on release/recapture data (Urquhart & Urquhart 1978, Urquhart 1987) depict their contention that eastern monarchs normally proceed in a southwest direction in fall, directly (more or less) on course to the Mexican wintering grounds. This would, therefore, take most northeastern monarchs on an inland path away from the coast. But their release/recapture data (Urquhart & Urquhart 1978) also indicate that a substantial number of migrants move east—or southeastward and this, they say, can be accounted for by strong westerly and northwesterly winds. Furthermore, they maintained that these "aberrant" monarchs probably end up in locations other than the known wintering sites (Urquhart 1987:141). There is substantial evidence (Gibo 1986, Schmidt-Koenig 1993), including data from the Urquharts (1979), that migrating monarchs are affected by wind drift during migration, and so we consider it unreasonable to conclude that most wind-drifted individuals are necessarily off-course, or that their destination must differ from the main cohort of eastern monarchs. Point to point release/recapture data establish relatively little, if anything, about either the actual tracks taken by individual monarchs or the mean track of the whole migrant population. It seems just as reasonable to hypothesize that large numbers of northeastern monarchs normally move southeastward to the coast and then continue moving southward. In short, we simply do not know what precise course any

individual monarch or group of monarchs takes on its way to the Mexican wintering grounds.

Do hawks and monarchs use a similar migration strategy along the Atlantic coast? Broad-winged hawks, *Buteo platypterus* Vieillot (Accipitridae), are common summer residents of northeastern forests. These hawks overwinter in Central and South America, south to Chile, and considerable research has been done on their migration phenology and flight dynamics (Kerlinger 1989, Dodge 1985–1994). Interestingly, both this hawk and the monarch often are seen migrating together in the fall, and both employ thermal soaring and gliding flight during their migration (Kerlinger 1989, Gibo & Pallett 1978).

One model for the migration of the broad-winged hawk, given by Kerlinger et al. (1985), suggests elliptical migration paths. Such routes would allow these hawks to take advantage of prevailing westerly winds in the northern latitudes of North America, and then the prevailing easterly winds in the southern latitudes. Kerlinger et al. (1985) hypothesize that this would result in a quicker and more energetically efficient departure from the northern portion of their range to the region of 35°N (the approximate latitude of Cape Hatteras, North Carolina on the east coast), where the hawks then could begin to take advantage of the prevailing easterlies. Monarchs may employ a similar strategy, and thus *initially* move eastward toward the coast in the northern portions of their range.

Such a strategy would be consistent with Gibo's (1986) hypothesis that there are two major, potentially conflicting, selective pressures on monarchs migrating south in southern Ontario. First, there is selection to minimize effort, and second, there is selection to escape the high latitudes as quickly as possible. Of these two strategies, Gibo maintained that a rapid exiting from the north is often the more important. Migrating with NE tail winds would best allow for a straight-line path to the overwintering sites and would be the optimal response to both selection factors. However, fall weather systems with a westerly wind component are typical of this region. Thus, when monarchs move south under the influence of the prevailing winds, there is a concomitant easterly movement. Gibo found that southward migrating monarchs ignore right crosswinds (N, NW, or W winds), but compensate for left crosswinds (E, SE, and S winds). These behaviors are consistent with an energy efficient and rapid exit from the north, and, if the monarchs avoid flying out over the Atlantic, would lead to the fall build-ups along the east coast. That this is typical monarch behavior is supported both by the historical accounts and our new data.

There is little doubt that monarchs migrating during the fall are affected by dynamic weather systems with their attendant winds. Indeed,

monarchs are, at times, blown off course with disastrous results (summary in Brower 1995). Such phenomena, however, need to be distinguished from the more typical events of this butterfly's travels. While more research needs to be done to furnish a definitive model of the monarchs' southward journey, the elliptical path hypothesis suggested by avian researchers may be a useful framework for understanding the annual fall migration path of monarchs along the Atlantic coast.

The future. A number of factors combine to affect the overall viability of the monarch's eastern migratory population—now considered an endangered biological phenomenon (Brower & Malcolm 1991). On the wintering grounds, abnormally cold winters, deforestation, and local disturbances all play a part (Malcolm & Zalucki 1993). Throughout the monarch's breeding areas and along its migratory routes, the availability of milkweeds, nectaring resources, and roost sites are critical factors. Coordinated, long-term quantitative monitoring projects at breeding areas, along the migratory routes, and at the overwintering sites will provide data that will allow us to document fluctuations in monarch numbers and, perhaps, begin to define factors critical to the conservation of this well-known butterfly's remarkable migration. Let us hope that the long term data do not substantiate the demise of the eastern migration as predicted in Brower and Malcolm (1991).

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LIGHT-TRAP CATCHES OF MOTHS WITHIN AND ABOVE THE CANOPY OF A NORTHEASTERN FOREST

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ABSTRACT. A catch of 10,991 moths, comprising 311 species in 15 selected families, was identified from two 22-watt blacklight traps operating for 29 nights between 21 June and 30 July 1990. Nightly catches ranged from 4 to 824 individuals per trap. In the within-canopy site, 6,088 individuals of 255 species were identified, whereas in the above-canopy site, 4,903 individuals of 269 species were identified. There were 213 species common to both sites. The coefficient of similarity (of species) between sites was 0.862 (Morisita-Horn index). The percentage complementarity between sites was 31.5 (Marczewski-Steinhaus distance).

Moths in the family Noctuidae dominated the identified catches, accounting for 43.5% of the species and 36.6% of the individuals within the canopy, and 49.4% of the species and 52.4% of the individuals above the canopy. Moths in the family Geometridae were the next most common identified group, forming 33% of individuals in the canopy and 26% of individuals above the canopy. Members of no other single family formed more than 8% of the identified individuals. Several non-tree-feeding species and four known migrants were collected only above the canopy.

Each trap's nightly catch was separated into 30-minute sequential samples, 16/night, between 2130–0530 h ADT. Individuals were trapped all night, but on average catches peaked at 2300–2330 h, two hours after sunset. On nights when a trap's catch exceeded 300 individuals, peak numbers occurred later than on nights when fewer individuals were trapped. When species inventory was summed over the 29 nights, full-night sampling, as opposed to partial-night sampling, was necessary to maximize the number of species. Species accumulation curves were steepest during the last week of June and shallowest during the first two weeks of July. Species richness was estimated as being between 309 and 312 species in the selected families (Chao 1 estimator) during the 29-night sample period.

Additional key words: 30-minute samples, within-night activity, partial-night samples, inventory, species richness.

Light traps are a common tool for elucidating the biology of moth species, and probably are the most widely used insect traps (Southwood 1978, Muirhead-Thomson 1991). They have been used for faunal surveys of both pest and non-pest moth species in the United Kingdom since 1933 (Taylor 1986). Sample et al. (1993) used light traps to evaluate the effect of insecticide spray on non-target Lepidoptera, and recent studies on diversity of moth communities using light traps include Magurran (1985), Robinson and Tuck (1993), Thomas and Thomas (1994).

In faunal surveys, questions arise with regard to sampling effort and detection of species. One such question is whether operating a light trap for only part of a night yields as many species as when a trap is operated throughout the night. Such partial-night sampling is attractive if a collection is being made from a sheet when the lamp is not incorporated into a trap (Profant 1989, Robinson & Tuck 1993), or when

many hundreds of moths are likely to be captured resulting in an inordinate amount of damage to specimens and time for sorting and identification (Sample et al. 1993, Thomas & Thomas 1994). Other questions relate to the total number of species in the area and the effort required to find them (Wolda 1983, Soberon & Llorente 1993, Colwell & Coddington 1994).

The present study was part of an ongoing analysis of the population dynamics of spruce budworm, *Choristoneura fumiferana* (Clemens) (Tortricidae), where light traps were used to detect migration of spruce budworm moths into the study plot. Many other species were trapped along with spruce budworm, and the objectives of this study were to compare, over a 29-night sample period: (1) the between-night light-trap catches of moths at two sites (within and above a forest canopy), based on number of individuals; (2) the average within-night light-trap catches of moths at the two sites, based on number of individuals and number of species captured during sequential 30-minute periods; (3) the similarity and complementarity of the catches at each site, based on numbers of species and individuals; (4) partial-night sampling with full-night sampling for species-inventory purposes; and (5) species accumulation curves between sites, and to estimate local species richness.

METHODS

Beginning on 21 June, and ending on 30 July 1990, two 22-watt black-light traps (Universal Light Trap, Bioquip Products, California) were operated in the Peter Brook study area of the Acadia Forest Experiment Station, near Fredericton, New Brunswick, Canada. For a variety of reasons, full-night trap data from both traps are available for only 29 of the potential 40 nights. A description of the study area is given in Thomas and Thomas (1994).

A within-canopy trap, with the lamp at 6.4 m above the ground, was on a platform, 3 × 1.5 m, on a tower within the closed crowns of balsam fir trees, *Abies balsamea* (L.) Miller (Pinaceae). The otherwise touching branches were trimmed to leave a clearing of 3 × 1.5 m. A blue plastic sheet, 1.8 × 2.4 m, was stretched above the platform at a height of 2.4 m above the lamp. This sheet made direct observation of the lamp impossible from above, although the reflection of the light off the foliage of adjacent trees gave a glow to the immediate area that was obvious from the ground. An above-canopy trap was on a tower with the lamp at about 1 m above the tips of the tallest trees in the immediate vicinity (lamp at 9.5 m above the ground). This trap was on a platform similar to that of the within-canopy trap but had no plastic sheet above it.

The lamp was above the rim of the aluminum collecting funnel in the within-canopy trap, and below it in the above-canopy trap. The

TABLE 1. Total number of identified species trapped by family, and number and percentages of species and moths by site (excludes uncounted numbers of all other families). Geometridae excludes *Eupithecia* spp., and the spruce budworm is the only recorded taxon in Tortricidae.

Family	Total species	Within-canopy site: Species Number	Within-canopy site: Species %	Within-canopy site: Moths Number	Within-canopy site: Moths %	Above-canopy site: Species Number	Above-canopy site: Species %	Above-canopy site: Moths Number	Above-canopy site: Moths %
Hepialidae	1	1	0.39	3	0.05	1	0.37	1	0.02
Sesiidae	1	1	0.39	11	0.18	1	0.37	27	0.55
Cossidae	1	1	0.39	1	0.02	0	—	—	—
Tortricidae	1	1	0.39	450	7.40	1	0.37	192	3.92
Limacodidae	4	4	1.57	64	1.05	3	1.12	24	0.49
Thyatiridae	2	1	0.39	3	0.05	2	0.74	6	0.12
Drepanidae	3	3	1.18	50	0.82	2	0.74	36	0.73
Geometridae	86	79	31.00	2012	33.00	67	24.90	1273	26.00
Lasiocampidae	3	2	0.78	163	2.68	3	1.12	62	1.26
Saturniidae	4	3	1.18	40	0.66	3	1.12	29	0.59
Sphingidae	10	7	2.75	103	1.69	10	3.72	57	1.16
Notodontidae	27	23	9.02	444	7.29	24	8.92	369	7.53
Arctiidae	18	16	6.27	441	7.24	15	5.58	221	4.51
Lymantriidae	4	2	0.78	76	1.25	4	1.49	36	0.73
Noctuidae	146	111	43.50	2227	36.60	133	49.40	2570	52.40
Totals	311	255		6088		269		4903	

effect of these configurations was that the lamp of the within-canopy trap was potentially visible horizontally (although partially restricted by the fir foliage), but the lamp of the above-canopy trap was visible only from above the forest. The towers were 76 m apart with the base of the above-canopy tower at a slightly higher elevation than the remainder of the study plot. The lamps were switched between traps on alternate nights.

Each trap was equipped with an automatic time-interval collecting device (King et al. 1965, Siddorn & Brown 1971, Smith et al. 1973). Each trap's nightly catch was separated into 16 sequential samples of 30-minute duration. The lamps were switched on at 2130 h and switched off at 0530 h. Sunset and sunrise were at 2120 h and 0536 h on the first trap-night and 2058 h and 0606 h on the last. However, the sky was noticeably lighter at 30 min before sunrise and stayed light for 30 min after sunset.

All individuals in 14 of the 15 selected lepidopteran families listed in Table 1 (see also Appendices I and II) were identified to species and counted, except for *Eupithecia* spp. (Geometridae) which were not included in any totals. For Tortricidae, only spruce budworm moths were identified and counted. Further details of moth identification are given in Thomas and Thomas (1994). Data analysis was based on 311 species, although there were at least two additional species present. *Syngrapha*

alias (Ottolengui) (Noctuidae) and *Syngrapha abstrusa* Eichlin and Cunningham (Noctuidae) had identifications confirmed from male genitalia but many individuals were females that I could not positively identify. Thus, the 54 individuals that were recorded as one species (*S.* "*alias*") included both *alias* and *abstrusa.* Klaus Bolte identified 10 individuals of *Hydriomena renunciata* (Walker) (Geometridae) and 17 individuals of *Hydriomena divisaria* (Walker) (Geometridae). I could not assign a further 126 individuals to either taxon and thus the 153 individuals were listed as one species (*H.* "*renunciata*"). It is also possible that the 44 individuals identified as the single species *Xestia dolosa* Franclemont (Noctuidae) could be *Xestia adela* Franclemont (Noctuidae) or a mix of both species. Similarly, the 232 individuals recorded as *Hypagyrtis piniata* (Packard) (Geometridae), could be *Hypagyrtis unipunctata* (Haworth) (Geometridae) or could include both species. I have reared *H. piniata* from larvae collected at the study plot.

No detailed weather data were measured except for a continuous temperature reading at the within-canopy trap. The total numbers of individuals, in the selected families, caught in each trap per night were counted and the actual numbers were used for between-night comparisons. Descriptions of the within-night moth activity were based on geometric means. The numbers of individuals caught during a 30-minute time-period were transformed as log(catch+1) and considered as one replicate for that time-period. When these log values were added together and divided by the number of trap-nights (n=29), the geometric mean catch for a time-period could be calculated by subtracting 1 from the antilog of the mean log value. These geometric means gave a measure of the abundance of individuals trapped at each time-period and also the distribution of catches during the night. Such an averaging of the catch per time-period over the 29 nights ensured that activity patterns during nights of small catches were not overshadowed by nights with large catches (Williams 1935, 1937, 1939, 1951, 1964, Williams et al. 1955, Hardwick 1972, Bowden & Gibbs 1973, Persson 1976, Douthwaite 1978, Zar 1984). The within-night distribution of species was determined simply by accumulating all the species trapped during each 30-minute period over the 29 nights. The accumulated number of species for each summed 30-minute period was plotted as the percentage of the total number of identified species collected at the site.

The two sites were compared for similarity of species by determining the Morisita-Horn index for coefficient of similarity (Wolda 1981, Magurran 1988), and the complementarity of the two species lists was determined using the Marczewski-Steinhaus distance (Colwell & Coddington 1994). The former index takes into account the relative abundance of the species in each trap while the latter uses the number of

species in common between the two traps and the number of species unique to either trap. A similarity index of unity would be expected from two random samples (each of about 5,000 moths) drawn from the same population (see Wolda 1981, Fig. 4). An index of zero would occur if the traps had no species in common. Complementarity of two species lists varies from zero when the lists are identical, to unity when the lists are totally distinct.

The effect of partial-night sampling on the species inventory was determined in the following manner. It was assumed that sampling would begin at dusk and end before dawn. Species were summed by time-period beginning with the total number of species collected during the 29 replicates of time-period 1. Species collected during all 29 replicates of time-period 2 that were not collected during time-period 1 were considered "new." These "new" species from time-period 2 were summed. Similarly, "new" species collected during all 29 replicates of time-period 3 were summed, followed by "new" species from time-period 4, etc. The results are presented as bar charts of the number of "new" species versus time-period. The "loss" of species caused by any curtailment of collecting before dawn could be readily determined.

The number of species was accumulated chronologically by adding each night's catch, from one trap, to the accumulated catch for that trap. This cumulative number of species was plotted against the sample date to get a species accumulation curve for each site (Colwell & Coddington 1994). An estimate of the potential richness of the sites for the sample period was determined using the Chao 1 estimator. This method involves squaring the number of singletons (i.e., the number of species represented by a single individual), dividing it by twice the number of doubletons and adding this estimate of undetected species to the number of collected species (Colwell & Coddington 1994). This estimator performs especially well when there is a preponderance of relatively rare species (Colwell & Coddington 1994) as is the case with the present data set (Appendices I & II; see also Thomas & Thomas 1994, Table 2).

RESULTS

A total of 10,991 individuals representing 311 species in 15 selected families was identified from the two sites. The 6,088 individuals in the 255 species identified from the within-canopy site have been listed, along with the extreme dates of capture and numbers of specimens, in Thomas and Thomas (1994). A total of 4,903 individuals in 269 species was identified from the above-canopy site and are listed, with extreme dates and numbers, in Appendix I. This list identifies the 213 species that were common to both sites and the 56 species that were unique

to the above-canopy site. Appendix II lists the 42 species that were unique to the within-canopy site.

The breakdown of the selected catches into numbers of species and individuals per family, with these numbers as percentages of totals, for each site is shown in Table 1. Members of the families Noctuidae and Geometridae formed the bulk of the identified catch in each trap. Within the canopy: noctuids accounted for 43.5% of the identified species, and with 36.6% of the identified individuals formed the largest single-family catch; geometrids with 31.0% of the identified species and 33% of the identified individuals formed the second largest single-family catch. Above the canopy: noctuids formed 49.4% of the identified species and accounted for 52.4% of the identified individuals; geometrids with 24.9% of the identified species and 26.0% of the identified individuals were again the second largest single-family. Members of the other 12 selected families (i.e., families other than Tortricidae) were relatively rare at each site, with members of no single family forming more than 8% of the total individuals.

Night vs. size of catch. The total number of individuals captured each night varied between 34 and 1,372 with the three lowest catches occurring on nights having the lowest temperatures (9–11°C) (Table 2). The size of a night's catch at each site was usually similar with the differences in the numbers of individuals trapped between sites being less than three-fold on 24 nights. On the remaining five nights (26/27 June, 5/6 July, 6/7 July, 10/11 July, 17/18 July) the within-canopy catch was greater than four times that of the above-canopy catch (Table 2). Greater variation in catch size was seen in the above-canopy site (ranging from 4 to 824 individuals/night), than in the within-canopy site (30 to 548 individuals/night).

Within-night activity: individuals. The pattern of the within-night catches, based on the geometric mean number of individuals per time-period, was similar at each site. There was a rapid build-up in numbers from low during time-period 1 (2130–2200 h), to high during time-period 4 (2300–2330 h) that was followed by a gradual decrease in numbers until time-period 16 (0500–0530 h) (Fig. 1). When the nightly catches were grouped, based on catch size, the activity patterns differed within and between sites:

i. Within-canopy site. On the seven nights when the catches exceeded 300 individuals per night, numbers peaked late and were maintained for a longer period than on nights when catches were lower (Fig. 2A). This catch pattern was associated with nights when average temperature was 19.4°C at 2400 h. On the eight nights when catches were between 201 and 300 individuals, the catch pattern was similar to that of the high-catch nights, with many individuals flying in the middle of the night

TABLE 2. Numbers of identified moths trapped above and within the canopy on 29 nights. Temperature in degrees Celsius, as recorded at 2400 h.

		Number of individuals			
Day of year	Date	Above	Within	Total	Temperature
172	21/22 June	114	278	392	12
176	25/26	149	260	409	15
177	26/27	71	347	418	18
178	27/28	824	548	1372	16
179	28/29	45	126	171	12
180	29/30	233	264	497	14
183	02/03 July	62	105	167	13
185	04/05	345	313	667	19
186	05/06	8	37	45	9
187	06/07	4	30	34	10
189	08/09	146	125	271	14
190	09/10	60	53	113	17
191	10/11	30	161	191	17
192	11/12	21	37	58	11
193	12/13	75	114	189	13
194	13/14	76	160	236	13
195	14/15	99	279	378	20
196	15/16	462	369	831	21
197	16/17	237	251	488	23
198	17/18	57	327	384	20
199	18/19	294	345	639	22
200	19/20	192	254	446	21
201	20/21	234	278	512	19
202	21/22	50	132	182	16
203	22/23	104	80	184	15
204	23/24	105	100	205	17
205	24/25	411	393	804	20
206	25/26	270	235	505	19
210	29/30	116	87	203	23

(Fig. 2A). The average temperature on these nights was 17.9°C at 2400 h. When a night's catch was between 101 and 200 individuals (n=8 nights), there was still a rapid build-up in numbers as seen in the "big-catch" nights but there was a sharp drop in numbers after 2330 h (time-period 4) (Fig. 2A). On these nights, the average temperature was 14.0°C at 2400 h. When the nightly catches were low (<101 individuals/night, n=7 nights), cathes remained at a constant low level after 2300 h (time-period 3) (Fig. 2A). The temperature averaged 14.6°C at 2400 h.

ii. Above-canopy site. When nightly catches totalled >300 individuals (n=4 nights), the mean number of individuals per time-period increased rapidly and remained high from 2230 h to 0300 h (time-periods 3 to 11) (Fig. 2B). The average temperature was 19.0°C at 2400 h. When nightly catches were between 201 and 300 individuals/night (n=5 nights), the mean number of individuals per time-period increased slowly and did not reach a plateau until after 2400 h (time-period 6) (Fig.

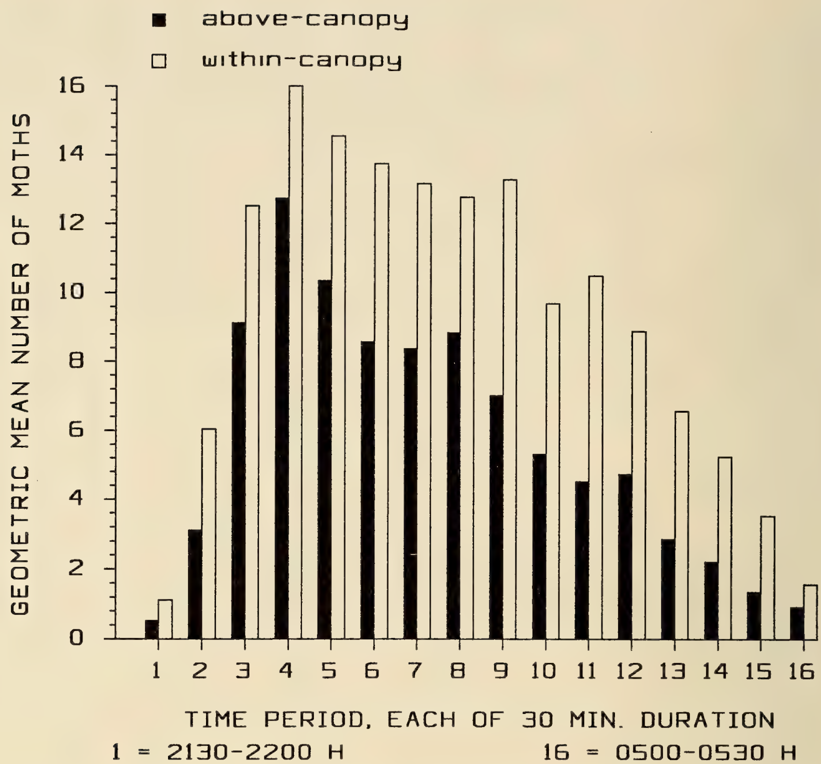

FIG. 1. Average within-night light-trap catch pattern of individuals above and within the canopy. Each bar represents the geometric mean catch of twenty nine 30-minute periods. Sunset and sunrise were at 2120 h and 0536 h on the first trap-night and 2058 h and 0606 h on the last.

2B). The average temperature was 19.4°C at 2400 h. The pattern of the catch of individuals on nights when the catch was between 101 and 200 individuals/night was markedly different from the pattern seen in the within-canopy trap for this grouping of individuals (Fig. 2B). There was no rapid rise in numbers and the mean catch per time-period stayed at a relatively constant low level throughout the night. The average temperature was 16.7°C at 2400 h on these seven nights. On the 13 nights when catches were low (<100 individuals/night) the mean catch per time-period remained constant throughout the night and the temperature averaged 15.0°C at 2400 h.

An examination of the average within-night catch pattern for single species that had sufficient numbers of individuals to detect a pattern, showed that individuals of most species were trapped throughout the eight-hour night. Also, peak catch occurred early in the night, as in e.g.,

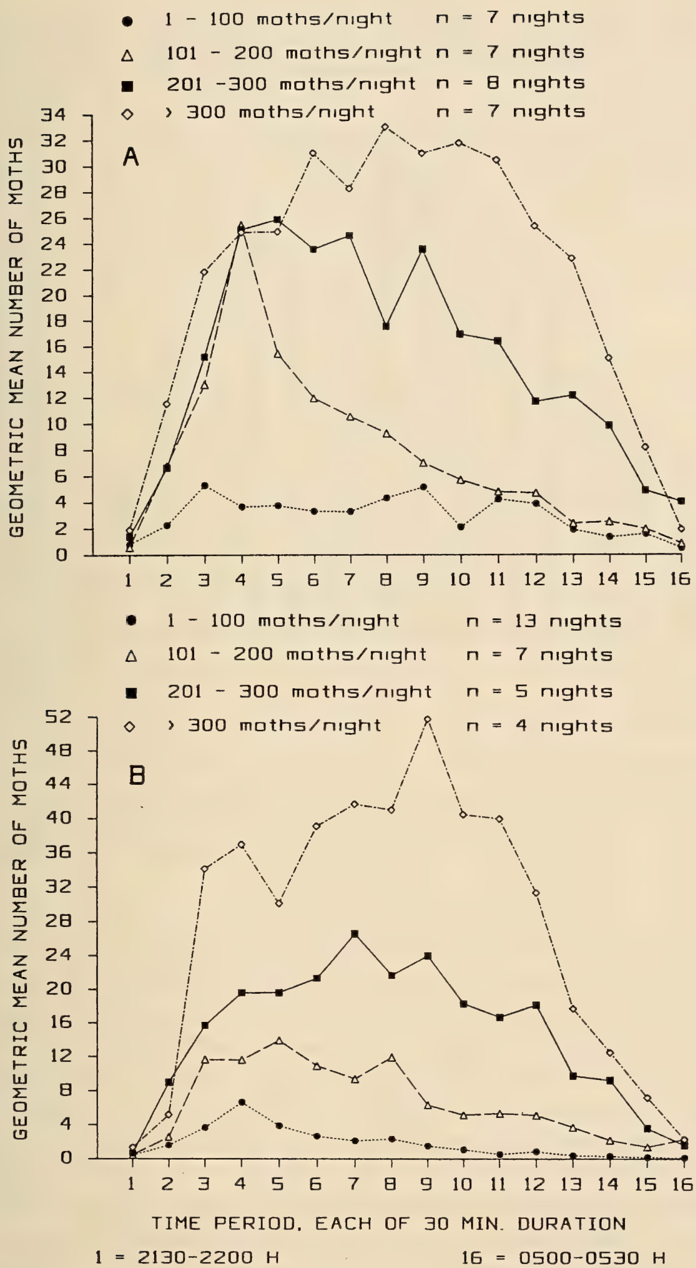

FIG. 2. Average within-night catch patterns of individuals when nights are grouped by size of catch. A: within-canopy site; B: above-canopy site.

TABLE 3. Geometric mean number of individuals trapped per 30-minute period for *Elaphria festivoides* (9681) and *Malacosoma disstria* (7698) in the above-canopy trap (A) and the within-canopy trap (W). All numbers multiplied by 100 to remove decimals. Maxima in bold.

		Mean number of individuals/time-period (× 100)															
Species	Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
9681	A	7	59	112	**117**	65	35	6	21	16	20	15	4	7	7	0	0
9681	W	7	33	41	**72**	39	28	33	21	7	26	12	9	7	4	9	7
7698	A	0	8	8	12	8	23	16	33	**46**	12	18	12	8	12	4	0
7698	W	4	16	16	24	35	23	55	67	**87**	66	42	29	8	12	6	0

Elaphria festivoides (Gn.) (Noctuidae) whose members were trapped in all time-periods but whose numbers peaked between 2300 and 2330 h (time-period 4) (Table 3). A few species showed peak catches later in the night, e.g., *Malacosoma disstria* Hbn. (Lasiocampidae) at 0130–0200 h (time-period 9) (Table 3), whereas *Acronicta retardata* (Wlk.) (Noctuidae) had peak catches at 0200–0230 h (time-period 10). There was usually no difference in average catch patterns between the two sites for individuals of the same species (Table 3).

Within-night activity: species. The number of species captured during each summed time period is shown as a percentage of the total number of species captured at that site (Fig. 3). For example, 132 species were trapped during the 29 nights between 2330 h and 2400 h (time-period 5) in the within canopy trap. These 132 species represented 51.8% of the total species (n=255) taken within the canopy. The percentage of the species captured was similar for both sites. There was a rapid increase in the number of species collected in subsequent summed 30-minute sampling periods, from about 7% of the total species between 2130–2200 h (the summed 29 samples from time-period 1) to about 44% at 2300–2330 h (the summed 29 samples from time-period 4). This proportion stayed at a plateau until 0200–0230 h (time-period 10) and then declined. Thus, a 30-minute collection taken on each of the 29 nights between 2300 h and 0230 h would have resulted in about 44–50% of the total species being collected. After 0230 h the number of species in each summed 30-minute collection began to decline until 0500–0530 h (time-period 16) when only 14% of the species were collected.

Similarity of catches between sites. In general, comparison of single-species catches between sites showed no great differences in numbers of individuals trapped, although more individuals were usually taken at the within-canopy site (Appendix I). Moths identified as *Hypagyrtis piniata* (Pack.) (Geometridae) were an exception in that they were taken five times more frequently within the canopy (193 vs. 39).

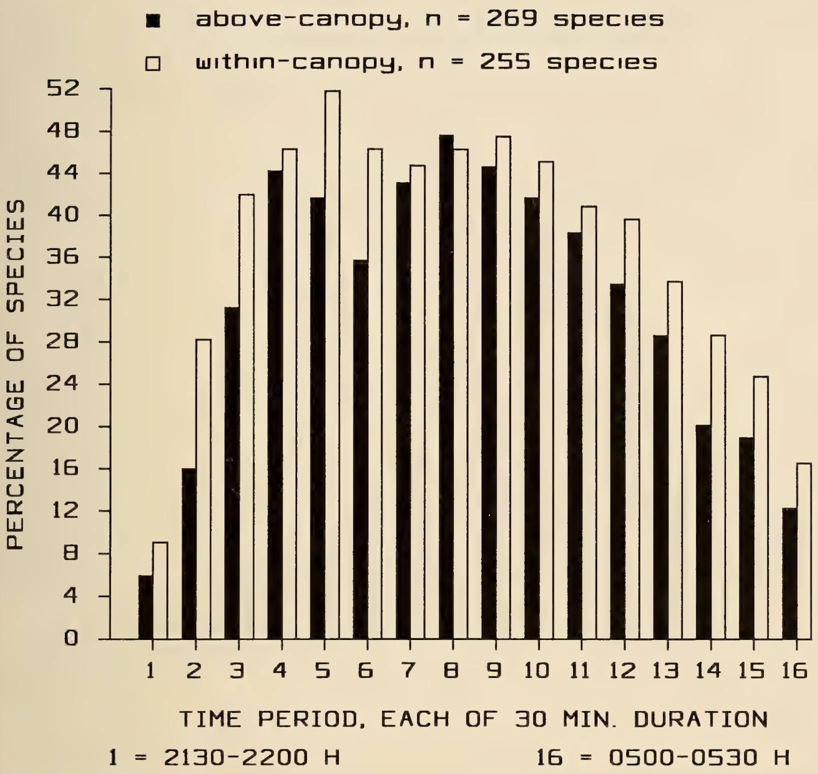

FIG. 3. Average within-night light-trap catches of numbers of species from 464, 30-minute samples per trap between 21/22 June and 29/30 July. Numbers are expressed as percentages of total species trapped at each site.

In contrast, *Callopistria cordata* (Ljungh) (Noctuidae) was 2.7 times more common above the canopy (438 vs. 162). Of the 213 species that were common to both sites, 134 species (63%) were trapped as frequently or more freqently within the canopy (i.e., 50% or more of their members were taken within the canopy). When the 42 species that were unique to the within-canopy site were added, there was a total of 176 species that were more frequent at this site. Of the species common to both sites, 79 (37%) were trapped more frequently above the canopy. Adding the 56 that were unique to this site, each of which was represented by <10 moths, gave a total of 135 species. The five most frequently trapped species of these 56 had larval food plants other than forest trees (Covell 1984): *Sideridis maryx* (Guenee) (Noctuidae) (n=9), food plant unrecorded, but not known to feed on trees (Prentice 1962); *Anticlea multiferata* (Walker) (Geometridae) (n=7), larvae feed on willow-herb; *Caenurgina crassiuscula* (Haworth) (Geometridae) (n=6), lar-

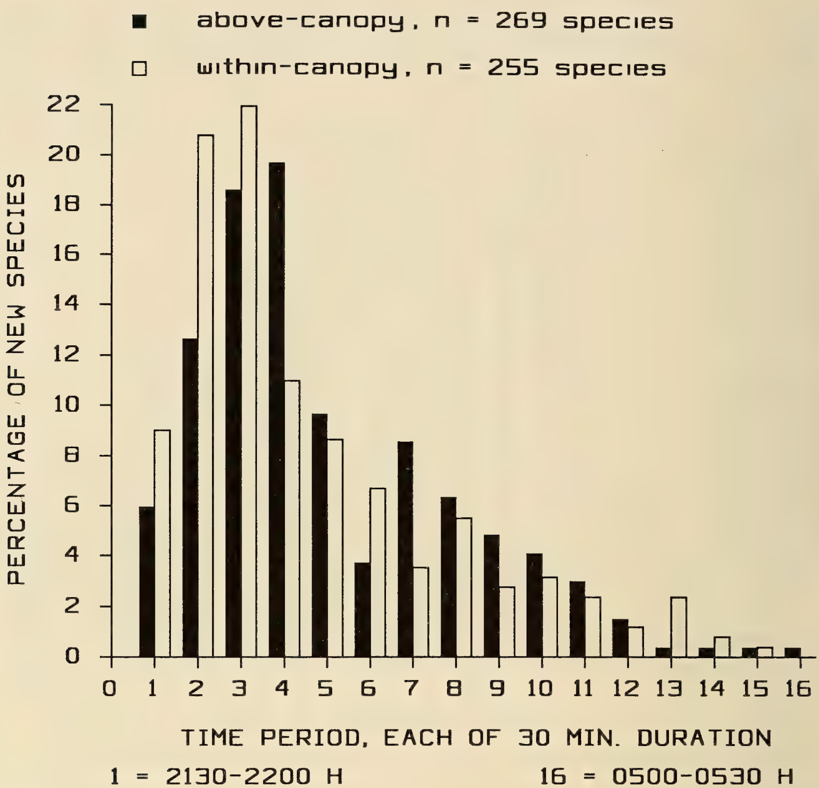

FIG. 4. Average within-night distribution of species new to the inventory based on 464, 30-minute samples per trap between 21/22 June and 29/30 July. Numbers are expressed as percentages of total species trapped at each site.

vae feed on clovers, grasses, lupines; *Apamea lignicolora* (Guenee) (Noctuidae) (n=6), larvae feed on grasses; *Apamea amputatrix* (Fitch) (n=6), larvae feed on ground plants. In addition, there were four species that are well known migrants (Chapman & Lienk 1981, Covell 1984): *Magusa orbifera* (Wlk.) (Noctuidae) (n=3); *Pseudaletia unipuncta* (Haw.) (Noctuidae) (n=2); *Agrotis ipsilon* (Hufn.) (Noctuidae) (n=2); and *Helicoverpa zea* (Boddie) (Noctuidae) (n=1).

Based on the total trap catches from the 29 nights, the Morisita-Horn index for coefficient of similarity between sites was 0.862 and the percentage complementarity between sites was 31.5.

Species inventory and sampling effort. The number of species new to the inventory, expressed as a percentage of total species for each site, is shown plotted over summed time-periods in Fig. 4. For example, 16 species were taken in time-period 1 (2130–2200 h) during the 29

TABLE 4. The number and cumulative percentage of "new" species during the night. Each time-period is based on the sum of 29 nightly samples between 21/22 June and 29/30 July.

		"New" species			
		Above-canopy		Within-canopy	
Time	Period	#	Cum. %	#	Cum. %
2130–2200	1	16	6.0	23	9.0
2200–2230	2	34	18.6	53	29.8
2230–2300	3	50	37.2	56	51.8
2300–2330	4	53	56.9	28	62.8
2330–2400	5	26	66.5	22	71.4
2400–0030	6	10	70.3	17	78.0
0030–0100	7	23	78.8	9	81.6
0100–0130	8	17	85.1	14	87.1
0130–0200	9	13	90.0	7	89.8
0200–0230	10	11	94.1	8	92.9
0230–0300	11	8	97.0	6	95.3
0300–0330	12	4	98.5	3	96.5
0330–0400	13	1	98.9	6	98.8
0400–0430	14	1	99.3	2	99.6
0430–0500	15	1	99.6	1	100.0
0500–0530	16	1	100.0	0	100.0

sample nights in the above-canopy trap. These 16 species represented just 6% of the total number of species (n=269) taken in this trap over the entire 29 sample nights. In the second time-period (2200–2230 h), 43 species were taken over the 29-night period in the above-canopy trap, of which 34 (12.6% of the total 269 species) had not been taken during time-period 1. Species new to the inventory increased until 2300–2330 h (time-period 4) and then declined rapidly. For the within-canopy site the number of "new" species increased until 2300 h, 30 min earlier than the above-canopy site, and then fell rapidly (Fig. 4). The cumulative percentage of "new" species for each site (Table 4) shows what effect the curtailment of nightly sampling effort would have had on species inventory. For example, if sampling had ceased at midnight on each of the 29 nights, 33.5% of the species (n=90) would not have been collected at the above-canopy site, and 28.6% (n=73 species) would have been missed at the within-canopy site. For all species to have been collected, sampling until dawn was necessary on all 29 nights.

Species accumulation curves. The shapes of the curves relating the cumulative number of species collected to the chronological sequence of sample dates were similar for both sites. Species were added rapidly during the last week of June, followed by addition at a much slower rate during the first two weeks of July, and then followed by another rapid increase in species during the last two weeks of July (Fig. 5).

Species richness. The estimated richness of each site for the sample

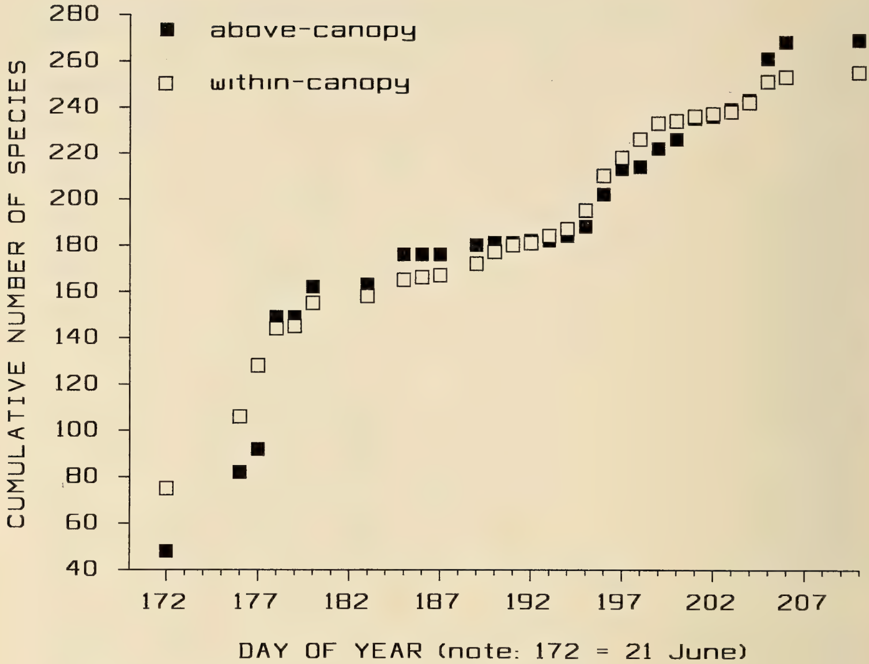

FIG. 5. Species accumulation versus sample date.

period (21 June to 29 July) was determined using the Chao 1 estimator. For the above-canopy site, 51 species were singletons and 30 were doubletons (Appendix I); the estimate of undetected species was thus 2601/60=43 for an estimated species richness of 312. For the within-canopy site there were 52 singletons and 25 doubletons (Appendices I & II), giving an estimate of 54 undetected species and an estimated species richness of 309. These figures are close to the 311 species trapped during the study period.

DISCUSSION

The differences in catch size between alternate nights was expected. Williams (1937) recorded similar differences for a trap catch involving many species and attributed them to changes in temperature, wind and other weather conditions. In a later study in which two types of trap were compared, it was found that the largest source of variation was the difference in catch size between nights (Williams et al. 1955). Several other studies documented large differences in catches between nights and attributed such differences to weather (wind speed, temperature, rainfall, relative humidity, night-length) moonlight, adult emer-

gence, and moth movement (Bowden 1982, Bowden & Church 1973, Dent & Pawar 1988, Morton et al. 1981, Nemec 1971, Tucker 1983).

In the present study, the factors affecting the size of a night's catch were unknown but weather was undoubtedly important. Apart from the continuous temperature reading at the the within-canopy trap, weather conditions and moonlight were not measured. Although high nightly catches (>300 individuals/trap) occurred only above 15°C, low nightly catches (<100 individuals/trap) occurred over the entire temperature range of 9–23°C (Table 2) suggesting that factors other than temperature were also affecting the size of the catch. In a detailed study of the influence of weather and nocturnal illumination on catches of noctuids in Australia, Persson (1976) concluded that night temperature, night wind and nocturnal illumination, in that order, were the most important factors influencing catch. However, 20% of the variance in catch could not be ascribed to local weather or illumination.

The within-night catches of individuals has been determined for several locations with the trapping period varying between 45–130 minutes. The shorter the time period, the greater the accuracy in showing the catch pattern throughout a night. Williams (1935, 1939) operated a trap throughout the year and divided the night into eight periods. This resulted in a catch period of 55 min in mid-summer to one of 110 min in mid-winter. Douthwaite (1978) used a mechanism to segregate the catch into hourly samples, but turned the light off for 15 min between each trapping period of 45 min so that moths attracted during one hour were less likely to be caught in the next. Graham et al. (1964) used 120-min periods during June and July and 130-min periods during August. Stewart et al. (1967), Mitchell et al. (1972), Persson (1976), Morton et al. (1981) and Dent and Pawar (1988) used 60-min periods. All these studies report on the within-night distribution of catches for individual species.

Three papers reported on within-night catches for multi-species data sets. Williams (1939) gave results for 74 moth species collected over a four year period in England. Graham et al. (1964) presented one graph based on 15,111 macrolepidoptera (unknown species number) collected during a three month period in Texas. Persson (1976) gave the hourly distribution, for each of 18 months, of a total catch of 339,000 noctuids in Australia. In each of these three studies, individuals were trapped all night but at different levels which resulted in a period of peak catch. In my study, individuals were also trapped throughout the night; there was a period of peak catch at each site (based on all individuals); and most species had the same catch pattern as the composite multi-species pattern.

Williams (1935) was the first to compare the within-night distribution

of insect catches in light traps on "good" and "poor" nights. He showed "that on the nights which had unusually large captures, the insects seemed to come later in the night, or rather kept up the numbers later, than on poor nights." The highest catches were associated with a high minimum temperature and a flat temperature gradient from dawn to dusk. This thesis was further supported in a later paper (Williams 1939). Persson's (1976) data showed a seasonal change in catch pattern which may be related to the same phenomenon. During the winter, peak catches of male noctuids occured within three hours of sunset; during the summer it occured six hours after sunset. In my study, the high-catch nights were associated with high temperatures and the maximum catch occurred later than on nights with small catches.

The observed within-night catch pattern of *Malacosoma disstria* can be compared with the data on this species from Ontario, Canada (Lewis et al. 1993). The catch patterns were very similar—low in the first part of the night with a peak in the middle of the night. However, in Ontario peak catches occurred 3–4 h after sunset, whereas in my study catches peaked in the 30-minute period between 4 h 20 min and 4 h 50 min after sunset (time-period 9) (Table 3). I can offer no explanation for this difference.

The similarity index of 0.862 is lower than expected for two random samples drawn from the same population (see Wolda 1981, Fig. 4). At 31.5%, the complementarity index is also indicative of a difference in species between sites. Several lines of evidence point to there being a migratory component to the above-canopy catch, when compared with the within-canopy catch. These include: the greater number of species, coupled with fewer moths; the slower rate of increase in catch size coupled with the constant size of the catch throughout the night, particularly when nightly catches were in the 101–300 individual range (Fig. 2B); the capture of known migratory species; the greater numbers of *Callopistria cordata* (438 vs. 162), the larvae of which are fern feeders; and the presence of species normally associated with field habitats. The presence of 56 unique species at the above-canopy site is a strong argument for a migratory component at this site.

The all-species-catch pattern (Fig. 3) can be compared with the species accumulation pattern (Fig. 4). Although time-period 8 (0100–0130 h), when summed over the 29 nights, showed the greatest number of species (n=128, 47.6% of the total) for the above-canopy site (Fig. 3), only 17 (6.3%) had not been taken before 0100 h (Fig. 4). The data, when summed over 29 nights, show that "new" species were captured throughout the night and that any curtailment of sampling before dawn would have resulted in the "loss" of species. However, the return on investment (in terms of new species captured versus effort when col-

lecting from a sheet, or versus battery-drain when using a battery-operated lamp) diminished rapidly after 2400 h. About 70% of the species were captured during the first 2.5 hours (summed over 29 nights), to catch the remaining 30% required a further 5.5 hours (also summed over 29 nights).

The shapes of the curves relating the cumulative number of species collected to the chronological sequence of sample dates were affected by the typical progression of species in Nearctic latitudes—a flush of species in early summer, a trough in mid-summer, followed by another flush of species in late-summer. No similar quantitative data were found in the literature, but the pattern seen in this study matches the pattern I have seen during 20 years of light-trapping in New Brunswick.

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APPENDIX I. Species list with numbers of moths and extreme dates of capture for the above-canopy site. Species indicated with an asterisk (*) were unique to this site. The numbers in parentheses are the numbers of moths taken at the within-canopy site for comparison. For extreme dates of capture see Thomas & Thomas (1994). Identifications for *Hypagyritis piniata* (Pack.) are uncertain, and may include or consist entirely of *Hypagyrtis unipunctata* (Haworth); *Hydriomena renunciata* (Wlk.) includes *Hydriomena divisaria* (Walker); *Syngrapha alias* (Ottol.) includes *Syngrapha abstrusa* Eichlin & Cunningham; identifications for *Xestia dolosa* Franclemont are uncertain, and may include or consist entirely of *Xestia adela* Franclemont.

Hepialidae			
Korscheltellus gracilis (Grt.)	25 July	1	(3)
Sesiidae			
Synanthedon acerni (Clam.)	21 June–25 July	27	(11)
Tortricidae			
Choristoneura fumiferana (Clem.)	4–29 July	192	(450)
Limacodidae			
Tortricidia testacea Pack.	25 June–4 July	4	(4)
Tortricidia flexuosa (Grt.)	27 June–25 July	16	(40)
Lithacodes fasciola (H.-S.)	15–25 July	4	(7)
Thyatiridae			
Habrosyne scripta (Gosse)	21 June–18 July	4	(3)
**Pseudothyatira cymatophoroides* (Gn.)	16–18 July	2	—
Drepanidae			
Drepana arcuata Wlk.	27 June–23 July	12	(20)
Drepana bilineata (Pack.)	27 June–29 July	24	(25)
Geometridae			
Protitame virginalis (Hulst)	21 June–11 July	5	(9)
Itame pustularia (Gn.)	15–29 July	119	(183)
Semiothisa minorata (Pack.)	27 June–24 July	14	(17)
Semiothisa bicolorata (F.)	8–21 July	6	(4)
Semiothisa bisignata (Wlk.)	15–24 July	8	(8)
Semiothisa sexmaculata (Pack.)	27 June–25 July	9	(5)
Semiothisa signaria dispuncta (Wlk.)	21 June–25 July	469	(724)
Semiothisa pinistrobata Fgn.	25 June–18 July	7	(16)
**Semiothisa oweni* (Swett)	4 July	1	—
Semiothisa orillata (Wlk.)	21 June–8 July	5	(3)
Iridopsis larvaria (Gn.)	25 June–18 July	11	(26)
Ectropis crepuscularia (D. & S.)	29 June–25 July	6	(23)

APPENDIX I. Continued.

Protoboarmia porcelaria (Gn.)	4–29 July	5	(5)
Melanolophia canadaria (Gn.)	25–27 June	3	(6)
Eufidonia convergaria (Wlk.)	25 June–22 July	6	(12)
Biston betularia cognataria (Gn.)	21 June–24 July	32	(28)
Hypagyrtis piniata (Pack.)	27 June–25 July	39	(193)
Lomographa vestaliata (Gn.)	21 June–15 July	19	(30)
Cabera erythemaria Gn.	27 June–25 July	22	(41)
Cabera variolaria Gn.	21 June–25 July	10	(22)
**Euchlaena serrata* (Drury)	20–24 July	2	—
Euchlaena johnsonaria (Fitch)	16–25 July	4	(7)
Euchlaena irraria (B. & McD.)	27 June	2	(4)
Xanthotype urticaria Swett	27 June–4 July	3	(5)
Pero morrisonaria (Hy. Edw.)	25 June–4 July	5	(13)
Nacophora quernaria (J. E. Smith)	25 June–4 July	6	(4)
Campaea perlata (Gn.)	27 June–20 July	5	(12)
Tacparia detersata (Gn.)	21–27 June	5	(8)
Homochlodes fritillaria (Gn.)	21 June–15 July	7	(5)
Metanema inatomaria Gn.	29 June–21 July	3	(11)
Metanema determinata Wlk.	18 July	1	(4)
Metarranthis amyrisaria (Wlk.)	21 June–4 July	4	(3)
Metarranthis hypocharia (H.-S.)	21 June	1	(1)
Probole arnicaria (H.-S.)	25–27 June	5	(15)
**Plagodis kuetzingi* (Grt.)	26 June–14 July	4	—
Plagodis phlogosaria (Gn.)	27 June–4 July	5	(7)
Plagodis alcoolaria (Gn.)	26–29 June	2	(4)
Caripeta divisata Wlk.	25 June–29 July	49	(78)
Caripeta piniata (Pack.)	25 June–14 July	5	(9)
Caripeta angustiorata Wlk.	19–29 July	9	(22)
Besma endropiaria (G. & R.)	9 July	1	(6)
Sicya macularia (Harr.)	20–24 July	3	(3)
Eusarca confusaria Hbn.	24 July	1	(1)
Tetracis cachexiata Gn.	21–27 June	12	(39)
Nematocampa resistaria (H.-S.)	20–29 July	9	(39)
Nemoria mimosaria (Gn.)	4–15 July	2	(2)
Cyclophora pendulinaria (Gn.)	21 June–29 July	24	(47)
Scopula limboundata (Haw.)	27 June–24 July	25	(36)
Dysstroma citrata (L.)	4 July	1	(2)
Dysstroma walkerata (Pears.)	27 June–4 July	4	(4)
Dysstroma hersiliata (Gn.)	27 June–19 July	3	(3)
Eulithis explanata (Wlk.)	16–29 July	59	(55)
**Eulithis serrataria* (B. & McD.)	24 July	1	—
Hydriomena perfracta Swett	21–29 June	3	(2)
Hydriomena renunciata (Wlk.)	21 June–29 July	74	(79)
Hydria undulata (L.)	29 June–22 July	2	(2)
Spargania magnoliata Gn.	29 June	1	(1)
**Anticlea multiferata* (Wlk.)	25 June–10 July	7	—
**Xanthorhoe labradorensis* (Pack.)	16 July	1	—
Xanthorhoe abrasaria congregata (Wlk.)	25 June–15 July	3	(8)
Xanthorhoe ferrugata (Cl.)	26 June–20 July	8	(3)
Xanthorhoe lacustrata (Gn.)	26 June–18 July	3	(1)
**Epirrhoe alternata* (Muller)	26 June–22 July	2	—
Hydrelia lucata (Gn.)	21 June–19 July	7	(11)
Hydrelia inornata (Hulst)	25 June–20 July	6	(9)
Eubaphe mendica (Wlk.)	16–25 July	2	(4)
Lobophora nivigerata Wlk.	25 June–29 July	86	(63)

APPENDIX I. Continued.

Lasiocampidae			
**Phyllodesma americana* (Harr.)	25 June	1	—
Malacosoma disstria Hbn.	8–29 July	59	(136)
Malacosoma americanum (F.)	18–20 July	2	(27)
Saturniidae			
Dryocampa rubicunda (F.)	21 June–25 July	27	(31)
Antheraea polyphemus (Cram.)	27 June	1	(8)
**Hyalophora cecropia* (L.)	25 June	1	—
Sphingidae			
Ceratomia undulosa (Wlk.)	21 June	1	(2)
**Sphinx kalmiae* J. E. Smith	25 June–29 July	2	—
Sphinx gordius Cram.	21–27 June	4	(9)
Lapara bombycoides Wlk.	21 June–24 July	15	(18)
Smerinthus jamaicensis (Drury)	8–23 July	5	(14)
Smerinthus cerisyi Kby.	21 June	1	(2)
Paonias excaecatus (J. E. Smith)	27 June–25 July	8	(15)
**Paonias myops* (J. E. Smith)	21–27 June	2	—
Pachysphinx modesta (Harr.)	25 June–23 July	17	(43)
**Darapsa photos* (Cram.)	27 June–24 July	2	—
Notodontidae			
**Clostera albosigma* Fitch	25 July	1	—
Nadata gibbosa (J. E. Smith)	21 June–4 July	7	(16)
Peridea basitriens (Wlk.)	15–25 July	3	(2)
Peridea ferruginea (Pack.)	21 June–29 July	113	(150)
Pheosia rimosa Pack.	27 June–29 July	9	(8)
Odontosia elegans (Stkr.)	18 July	1	(2)
**Notodonta scitipennis* Walk.	4–16 July	3	—
Notodonta simplaria Graef	16–25 July	5	(7)
Gluphisia septentrionis Wlk.	21 June–23 July	20	(54)
Furcula cinerea (Wlk.)	25 June–15 July	6	(5)
**Furcula occidentalis* (Lint.)	18 July	1	—
Furcula modesta (Hudson)	13–25 July	24	(11)
Symmerista leucitys Franc.	27 June–2 July	3	(2)
**Dasylophia thyatiroides* (Wlk.)	27 June–18 July	3	—
Macrurocampa marthesia (Cram.)	29 June–29 July	4	(3)
Heterocampa umbrata Wlk.	21 June–4 July	14	(11)
Heterocampa biundata Wlk.	21 June–11 July	10	(24)
Lochmaeus manteo Doubleday	25 June–25 July	6	(3)
Schizura ipomoeae Doubleday	21 June–25 July	34	(29)
Schizura badia (Pack.)	21 June–21 July	3	(2)
Schizura unicornis (J. E. Smith)	27 June–24 July	7	(10)
Schizura leptinoides (Grt.)	27 June–25 July	17	(8)
Oligocentria semirufescens (Wlk.)	16–23 July	6	(3)
Oligocentria lignicolor (Wlk.)	27 June–29 July	69	(89)
Arctiidae	15–22 July	6	(22)
Eilema bicolor (Grt.)	16–25 July	18	(54)
Hypoprepia fucosa Hbn.	24 July	1	(31)
Holomelina laeta treatii (Glt.)	20 July	1	(1)
Holomelina aurantiaca (Hbn.)	20–25 July	2	(7)
Holomelina ferruginosa (Wlk.)	15 July	1	(1)
Pyrrharctia isabella (J. E. Smith)	25 June–2 July	4	(40)

APPENDIX I. Continued.

Spilosoma virginica (F.)	21 June–29 July	33	(39)
Hyphantria cunea (Drury)	21 June–29 July	102	(182)
Apantesis virguncula (W. Kby.)	29 June–24 July	7	(5)
**Apantesis williamsii* (Dodge)	15 July	1	—
Halysidota tessellaris (J. E. Smith)	19–25 July	3	(2)
Lophocampa maculata Harr.	21 June–6 July	39	(48)
**Cycnia oregonensis* (Stretch)	21 July	1	—
Ctenucha virginica (Esp.)	27 June–20 July	2	(4)
Lymantriidae			
**Dasychira dorsipennata* (B. & McD.)	21 July	1	—
**Dasychira vagans* (B. & McD.)	20 July	1	—
Dasychira plagiata (Wlk.)	27 June–29 July	23	(69)
Leucoma salicis (L.)	4–18 July	11	(7)
Noctuidae			
Idia americalis (Gn.)	29 June–29 July	17	(50)
Idia aemula Hbn.	4–25 July	12	(11)
**Idia lubricalis* (Gey.)	24 July	1	—
Zanclognatha protumnusalis (Wlk.)	13–16 July	2	(7)
Bomolocha baltimoralis (Gn.)	29 June–25 July	12	(11)
**Bomolocha palparia* (Wlk.)	2–19 July	4	—
Pangrapta decoralis Hbn.	26 June–29 July	20	(26)
**Metalectra quadrisignata* (Wlk.)	20 July	1	—
Parallelia bistriaris Hbn.	21 June	1	(5)
**Caenurgina crassiuscula* (Haw.)	23–25 July	6	—
Catocala sordida Grt.	23–29 July	8	(3)
**Diachrysia aereoides* (Grt.)	14–16 July	2	—
**Diachrysia balluca* Gey.	24 July	1	—
Chrysanympha formosa (Grt.)	20–25 July	4	(12)
Autographa precationis (Gn.)	24 July	1	(1)
**Autographa bimaculata* (Steph.)	25–29 July	2	—
Autographa mappa (G. & R.)	27 June–24 July	12	(1)
**Autographa ampla* (Wlk.)	24–25 July	3	—
Syngrapha altera (Ottol.)	27 June–21 July	6	(4)
Syngrapha octoscripta (Grt.)	24 July	2	(1)
Syngrapha epigaea (Grt.)	17–24 July	2	(2)
Syngrapha viridisigma (Grt.)	19–25 July	3	(2)
Syngrapha alias (Ottol.)	21 June-23 July	32	(22)
Syngrapha cryptica Eichlin & Cunningham	15–19 July	3	(1)
Syngrapha rectangula (W. Kby.)	4–29 July	14	(27)
**Plusia putnami* Glt.	15–16 July	3	—
Plusia venusta Wlk.	15–29 July	3	(2)
Maliattha synochitis (G. & R.)	4 July	3	(1)
Maliattha concinnimacula (Gn.)	27 June	2	(5)
Pseudeustrotia carneola (Gn.)	25 June–29 July	15	(21)
Leuconycta diphteroides (Gn.)	27 June–18 July	9	(14)
Panthea acronyctoides (Wlk.)	27 June–25 July	24	(47)
Panthea pallescens McD.	26 June–25 July	31	(29)
Charadra deridens (Gn.)	21–28 June	15	(21)
Raphia frater Grt.	21 June–29 July	169	(152)
Acronicta americana (Harr.)	21 June–29 July	38	(18)
Acronicta dactylina Grt.	8–25 July	23	(9)
Acronicta lepusculina Gn.	25 June–19 July	11	(3)

APPENDIX I. Continued.

Acronicta innotata Gn.	27 June–25 July	23	(19)
Acronicta tritona (Hbn.)	27 June–22 July	7	(3)
Acronicta grisea Wlk.	25 June–24 July	18	(18)
Acronicta superans Gn.	27 June–18 July	3	(1)
Acronicta hasta Gn.	26 June–4 July	2	(1)
Acronicta fragilis (Gn.)	27 June–24 July	10	(14)
Acronicta clarescens Gn.	25 June–29 July	181	(162)
Acronicta retardata (Wlk.)	25 June–24 July	84	(49)
Acronicta impleta Wlk.	29 June	1	(1)
Acronicta noctivaga Grt.	16–25 July	2	(2)
Acronicta impressa Wlk.	15–23 July	4	(1)
Acronicta oblinita (J. E. Smith)	27 June	1	(4)
Agriopodes fallax (H.-S.)	26 June–25 July	37	(29)
Harrisimemna trisignata (Wlk.)	14–19 July	4	(4)
Apamea verbascoides (Gn.)	18 July	7	(1)
**Apamea cariosa* (Gn.)	22 July	1	—
**Apamea lignicolora* (Gn.)	15–25 July	6	—
**Apamea amputatrix* (Fitch)	14–29 July	6	—
**Apamea dubitans* (Wlk.)	24 July	1	—
**Parastichtis discivaria* (Wlk.)	29 July	1	—
Amphipoea velata (Wlk.)	24–25 July	3	(3)
Euplexia benesimilis McD.	21 June–21 July	23	(36)
Phlogophora iris Gn.	27 June–23 July	8	(3)
**Enargia infumata* (Grt.)	20–22 July	2	—
**Enargia mephisto* Franc.	15 July	1	—
Chytonix palliatricula (Gn.)	25 June–25 July	40	(78)
Dypterygia rozmani Berio	27 June–21 July	3	(1)
Hyppa xylinoides (Gn.)	27 June–29 July	8	(4)
Nedra ramosula (Gn.)	27 June–25 July	3	(1)
Callopistria mollissima (Gn.)	25 June–25 July	16	(43)
Callopistria cordata (Ljungh)	25 June–29 July	438	(162)
**Magusa orbifera* (Wlk.)	23–24 July	3	—
Proxenus miranda (Grt.)	15 July	1	(1)
**Caradrina morpheus* (Hufn.)	18 July	1	—
Elaphria versicolor (Grt.)	21 June–18 July	112	(51)
Elaphria festivoides (Gn.)	25 June–24 July	189	(130)
Apharetra dentata Grt.	15–29 July	26	(24)
**Homohadena infixa dinalda* Sm.	24–25 July	3	—
**Cucullia postera* Gn.	27 June–24 July	4	—
**Cucullia omissa* Dod	26–27 June	2	—
**Sideridis congermana* (Morr.)	27 June–2 July	3	—
**Sideridis maryx* (Gn.)	21 June–20 July	9	—
Polia imbrifera (Gn.)	4–25 July	14	(6)
Polia purpurissata (Grt.)	24 July	1	(3)
Polia detracta (Wlk.)	27 June–4 July	3	(8)
Polia goodelli (Grt.)	25 June	1	(1)
Polia latex (Gn.)	21–27 June	45	(18)
Melanchra adjuncta (Gn.)	25 June–29 July	41	(25)
**Melanchra pulverulenta* (Sm.)	27 June	2	—
Melanchra assimilis (Morr.)	21 June–24 July	26	(12)
**Lacanobia atlantica* (Grt.)	24 July	1	—
Lacanobia subjuncta (G. & R.)	29 June–25 July	5	(1)
Spiramater grandis (Gn.)	21–29 June	11	(14)
Spiramater lutra (Gn.)	21 June–29 July	63	(89)
Lacanobia rugosa (Morr.)	27 June–24 July	3	(2)

APPENDIX I. Continued.

**Trichordestra tacoma* (Stkr.)	4 July	1	—
Trichodestra legitima (Grt.)	27 June–24 July	21	(10)
**Trichordestra lilacina* (Harv.)	18–24 July	3	—
Papestra biren (Goeze)	27 June	1	(1)
Lacinipolia lustralis (Grt.)	29 June–24 July	10	(17)
Lacinipolia anguina (Grt.)	21–27 June	2	(1)
Lacinipolia renigera (Steph.)	18–29 July	3	(1)
Lacinipolia lorea (Gn.)	27 June–25 July	5	(7)
Lacinipolia olivacea (Morr.)	25 July	1	(1)
**Pseudaletia unipuncta* (Haw.)	27–29 July	2	—
Leucania multilinea Wlk.	24–25 July	4	(8)
**Leucania commoides* Gn.	24 July	1	—
Leucania insueta Gn.	25 June–25 July	9	(24)
Leucania inermis (Fbs.)	27 June–24 July	4	(4)
Leucania pseudargyria Gn.	24 July	1	(1)
Homorthodes furfurata (Grt.)	27 June–29 July	71	(77)
Orthodes crenulata (Butler)	4–29 July	25	(18)
Orthodes cynica Gn.	21 June–29 July	128	(268)
**Agrotis ipsilon* (Hufn.)	27 June–2 July	2	—
Euxoa divergens (Wlk.)	11–24 July	3	(2)
**Euxoa tessellata* (Harr.)	25 July	1	—
Ochropleura plecta (L.)	26 June–29 July	27	(29)
**Diarsia rubifera* (Grt.)	24–29 July	4	—
Diarsia jucunda (Wlk.)	29 June–25 July	19	(23)
**Eurois occulta* (L.)	22–25 July	2	—
Eurois astricta Morr.	25–29 July	2	(5)
Xestia dolosa Franc.	14–29 July	34	(10)
Xestia oblata (Morr.)	22–24 July	3	(3)
Xestia elimata (Gn.)	16 July	1	(2)
Xestia badicollis (Grt.)	16–25 July	3	(5)
Aplectoides condita (Gn.)	25 June–19 July	17	(25)
Anaplectoides prasina (D. & S.)	27 June–25 July	15	(8)
Anaplectoides pressus (Grt.)	27 June–24 July	6	(4)
Eueretagrotis perattenta (Grt.)	27 June–24 July	7	(5)
Eueretagrotis attenta (Grt.)	27 June–29 July	71	(60)
Heptagrotis phyllophora (Grt.)	27 June–25 July	20	(39)
Cryptocala acadiensis (Bethune)	23–29 July	8	(4)
**Pyrrhia exprimens* (Wlk.)	27 June	1	—
**Helicoverpa zea* (Boddie)	25 July	1	—
Noctua pronuba L.	24 July	1	(3)

APPENDIX II. List of species unique to the within-canopy site. See Thomas & Thomas (1994) for extreme dates of capture and number of specimens.

Cossidae

Prionoxystus macmurtrei (Guer.)

Limacodidae

Packardia geminata (Pack.)

Drepanidae

Oreta rosea (Wlk.)

Geometridae

Itame brunneata (Thunb.)
Itame anataria (Swett)
Semiothisa aemulataria (Wlk.)
Semiothisa ulsterata (Pears.)
Semiothisa transitaria (Wlk.)
Euchlaena obtusaria (Hbn.)
Euchlaena marginaria (Minot)
Euchlaena tigrinaria (Gn.)
Tacparia atropunctata (Pack.)
Anagoga occiduaria (Wlk.)
Plagodis serinaria H.-S.
Scopula cacuminaria (Morr.)
Ecliptopera silaceata albolineata (Pack.)
Rheumaptera hastata (L.)
Rheumaptera subhastata (Nolcken)
Mesoleuca ruficillata (Gn.)
Perizoma basaliata (Wlk.)
Xanthorhoe iduata (Gn.)
Horisme intestinata (Gn.)

Saturniidae

Anisota virginiensis (Drury)

Notodontidae

Clostera apicalis (Wlk.)
Pelidea angulosa (J. E. Smith)
Heterocampa guttivitta (Wlk.)

Arctiidae

Haploa lecontei (Guer.-Meneville)
Platarctia parthenos (Harr.)
Cycnia tenera Hbn.

Noctuidae

Idia rotundalis (Wlk.)
Zanclognatha pedipilalis (Gn.)
Zanclognatha cruralis (Gn.)
Palthis angulalis (Hbn.)
Lomanaltes eductalis (Wlk.)
Spargaloma sexpunctata Grt.
Syngrapha microgamma nearctica Fgn.
Baileya ophthalmica (Gn.)
Lithacodia muscosula (Gn.)
Apamea cogitata (Sm.)
Oncocnemis riparia Morr.
Polia nimbosa (Gn.)
Xestia youngii (Sm.)

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ANOTHER NEW *EUPHYES* FROM THE SOUTHERN UNITED STATES COASTAL PLAIN (HESPERIIDAE)

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ABSTRACT. The taxon *Euphyes dukesi calhouni* Shuey, new subspecies endemic to Florida, is described. This subspecies is amply differentiated from *Euphyes dukesi dukesi* and the two taxa are allopatric. In northeastern Florida and southeastern Georgia, where their known ranges closely approach one another, there is almost no evidence of intergradation. *Euphyes dukesi calhouni* is limited to swamp habitats that support large stands of the sedge hostplants, various *Rhynchospora* and *Carex* species (Cyperaceae).

Additional key words: biogeography, wetlands, conservation.

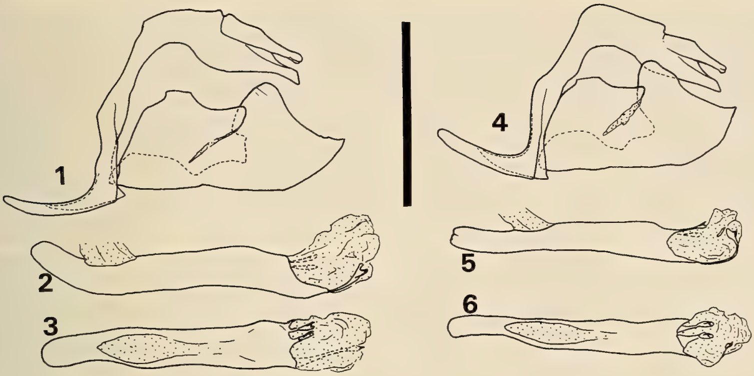
The southern Atlantic and Gulf Coastal Plains are rich regions for wetland butterflies, especially for genera such as *Euphyes, Poanes,* and *Problema.* For example, as currently known, eight named *Euphyes* species or subspecies occur in the wetlands of these coastal plains. Four of these taxa are restricted to the coastal plain: *Euphyes palatka palatka* (Edwards), *Euphyes palatka klotsi* Miller, Harvey and Miller, *Euphyes berryi* (Bell), and *Euphyes bayensis* Shuey.

Just as interesting as their limited coastal distributions is the presence in these wetland skippers of well differentiated peripheral populations, many of which have only recently been recognized and described. These peripheral populations are most probably the end result of allopatric differentiation. For example, *Euphyes palatka klotsi* represents its species on a few of the lower Florida Keys, separated from the nominate mainland subspecies by just tens of miles. *Euphyes bayensis,* a sister species to *Euphyes dion,* is presently known from a single locality on the extreme southern edge of the range of *E. dion.*

The purpose of this paper is to describe another distinctive peripheral *Euphyes,* to elaborate on the relationships between it and its closest relative, and to provide a summary of the ecology of the new taxon. Taxonomic methods are as described in Shuey (1988, 1993). Material examined specifically for this study included the holotype of *Euphyes dukesi* and additional specimens from Ohio, Indiana, Missouri, Louisiana, Mississippi, Alabama, Georgia, North Carolina, and Virginia as well as a series of unnamed *Euphyes* from peninsular Florida.

Euphyes dukesi calhouni Shuey, new subspecies

Description. Genitalia of both sexes typical for *Euphyes dion* Species Group (sensu Shuey 1993) (Figs. 1–14); ground color of both sexes dark brown, almost black (Figs. 15–18); male stigma typical *Euphyes* type (Shuey 1987), but surrounded by non-contrasting ground color and thus difficult to see without magnification and acute angle lighting; forewing wing fringe color identical to ground color; hindwing wing fringes slightly lighter;



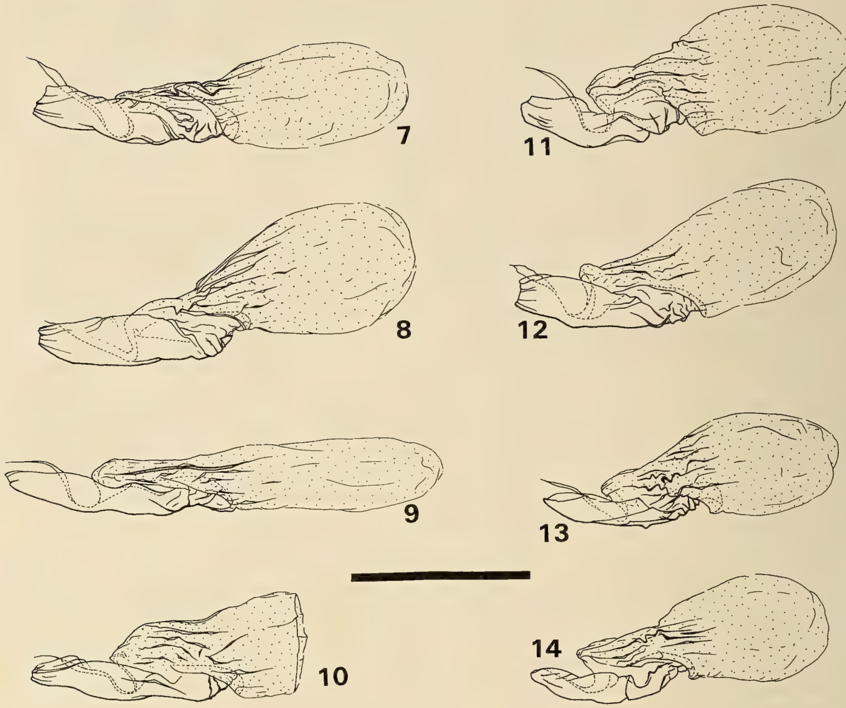
FIGS. 1–6. Male genitalia of *Euphyes dukesi* subspecies. 1–3, *Euphyes dukesi calhouni,* new subspecies, FL, Pasco Co., Cabbage Swamp 16 Sept. 1990; **1**, valva, tegumen, uncus, gnathos, vinculum and saccus (lateral view); **2**, aedeagus (lateral view); **3**, aedeagus (dorsal view). **4–6**, *Euphyes dukesi dukesi,* MO, St. Charles Co., St. Peters, 22 Aug 1982; **4**, valva, tegumen, uncus, gnathos, vinculum and saccus (lateral view); **5**, aedeagus (lateral view); **6**, aedeagus (dorsal view). Scale line=2 mm.

both sexes with olive-brown hairs dorsally at wing bases; both sexes with dark black ground color dominating ventral forewings, but costal region with dusting of olive-brown scales of same color as in dorsal hairs at wing base; neither sex with ventral forewing discal spot present in all other species of the *dion* Species Group; ventral hindwing mostly cool brown, with diffuse yellowish dash paralleling costa, running from wing base to wing margin; ventral hindwing veins yellow.

Types. *Holotype* ♀. Florida, Pasco Co., Cabbage Swamp, 16 September 1990, leg. J. V. Calhoun. *Allotype.* ♂. Florida, Pasco Co., Cabbage Swamp, 13 September 1990, leg. J. V. Calhoun. *Paratypes* (all Florida): Alachua Co., Gainesville, 25-IX-1978 (♀), leg. J. R. Slotten; Duval Co., Jacksonville, 25-IX-1978 (2♂,♀), 27-IX-1978 (♂), 1-X-1978 (♂), 8-X-1978 (♀), leg. H. D. Baggett; Flagler Co., Shell Bluff Landing nr San Mateo, 23-IX-1979 (♀), leg. J. R. Slotten; Hillsborough Co., I-275 at mile 57, 17-IX-1990 (2♂), leg. J. V. Calhoun; Pasco Co., Cabbage Swamp, 16-IX-1990 (♂,♀) leg. R. A. Anderson; Pasco Co., Cabbage Swamp, 13-IX-1990 (9♂,♀), 14-IX-1990 (♂), 16-IX-1990 (4♂,5♀), 17-IX-1990 (2♂), 18-IX-1990 (2♀), 26-IX-1990 (2♂,♀), leg. J. V. Calhoun; Seminole Co., Winter Springs, 5-VI-1983 (2♂,2♀), 17-IX-1983 (♂) leg. L. C. Dow. The holotype and allotype are deposited in the Carnegie Museum of Natural History.

Type locality. Florida, Pasco County, "Cabbage Swamp." The type locality lies in southern Pasco County on private property and is part of a larger wetland complex that extends into northern Hillsborough County along Cypress Creek. Cabbage Swamp is a hardwood-bald cypress swamp, dominated by water ash (*Fraxinus caroliniana* Mill), southern red maple (*Acer rubrum* L.), and bald cypress (*Taxodium distichum* [L.] Rich.). The understory has extensive stands of sedges, with *Rhynchospora inundata* (Oakes) Fern. dominating. Adult *E. dukesi calhouni* are closely associated with dense stands of *R. inundata* which is distributed in patches throughout Cabbage Swamp in areas where the water level reaches up to 0.5 m.

Etymology. This taxon is named after its discoverer, John Calhoun. While John was not the first to collect this butterfly, he was the first to grasp its significance and felt that he should document its local distribution, relative abundance, habitat requirements, and hostplants (details of his observations of *E. dukesi calhouni* appear in Calhoun 1995). This curiosity and drive is what separates John, and others like him, from more philatelically inclined collectors. My proposed common name is the "Florida Swamp Skipper." This name emphasizes both the endemic nature of the taxon and its primary ecological attrib-



FIGS. 7–14. Variation in female genitalia of *Euphyes dukesi* subspecies, all lateral views. 7–10, *Euphyes dukesi calhouni,* new subspecies; **7**, FL, Pasco Co., Cabbage Swamp, 13 Sept 1990; **8**, FL, Pasco Co., Cabbage Swamp, 16 Sept 1990; **9**, FL, Flagler Co., nr. San Mateo, 23 Sept 1979; **10**, FL, Seminole Co., Winter Springs, 5 June 1983. 11–14, *Euphyes dukesi dukesi*; **11,** OH, Logan Co., Test Track Swamp, 24 Jul 1983; **12**, VA, Chesapeake, 14 Aug 1967; **13**, MS, Sunflower Co., NE Moorhead, 19 Sept 1973; **14**, OH, Paulding Co., Miami Canal, 9 July 1960. Scale line=2 mm.

ute. Pyle (1981) somewhat inappropriately suggested the same common name for *Euphyes berryi,* a wetland species which is not endemic to Florida and which is found in open wetlands, not swamps.

Comparison of taxa. *Euphyes dukesi calhouni* can easily be separated from *E. d. dukesi* as follows (see Figs. 15–22):

1. Ground color: the ground color in *E. dukesi calhouni* is darker, almost approaching black, whereas in *E. d. dukesi* the ground color is dark brown (and in males contrasts with the black stigma).

2. Dorsal wings: in *E. dukesi calhouni,* the overscaling near the wing bases consists almost entirely of olive-brown hairs and extends slightly over half way across the hindwing and one-fourth of the way across the forewing; the scales covering the wings are black. In *E. d. dukesi,* the overscaling is composed of orange-brown hairs near the wing margin, but orange-brown scales predominate nearer the discal areas and extend two-thirds of the way across the hindwing and over half way across the forewing. Females of *E. d. dukesi* usually have two yellowish spots in the discal region of the forewing which are not present in *E. dukesi calhouni.* In some populations of *E. d. dukesi,* notably from Virginia and the lower Mississippi Valley, approximately 20% or more of the females lack all traces of these discal spots; these can be separated from *E. dukesi calhouni* by the presence of orange-

FIGS. 15–22. Adult *Euphyes dukesi calhouni,* new subspecies, and *Euphyes dukesi dukesi.* 15–18, *Euphyes dukesi calhouni* new subspecies; **15–16**, male, FL, Pasco Co., Cabbage Swamp, 13 Sept 1990 (dorsal and ventral); **17–18**, female FL, Pasco Co., Cabbage Swamp, 16 Sept 1990 (dorsal and ventral); 19–22, *Euphyes dukesi dukesi*; **19–20**, male, GA, McIntosh Co., Little Champy Road Waterfowl Sanct., 19 May 1979 (dorsal and ventral); and **21–22**, female, OH, Logan Co., Test Track Swamp, 16 July 1983 (dorsal and ventral).

brown scales on the dorsal hindwing and the more extensive light color of the hindwing fringes of *E. d. dukesi.*

3. *Ventral forewing:* in *E. dukesi calhouni,* the forewing of both sexes is almost black with olive-brown overscaling that follows the costa and wraps around the wing tip; the discal area is unmarked. In *E. d. dukesi,* the ground color is likewise almost black, but the overscaling is heavier, more extensive, and is orange-brown and contrasts strongly with the ground color. In *E. d. dukesi,* there is usually a well defined yellow spot in the discal region, although in some males this is reduced to a faint trace and may be entirely absent in some females. This spot is absent in *E. dukesi calhouni* (with one exception discussed below).

4. *Ventral hindwing:* in *E. dukesi calhouni,* the elongated yellow dash which extends outward from the wing base between veins M_1 and M_2 is diffuse and often dissipates before reaching the wing margin; the yellow dash between veins Cu_2 and 2A is usually absent. In *E. d. dukesi,* both of these yellow dashes are usually heavily scaled and extend boldly toward the margin in fresh specimens.

5. *Wing fringe:* the wing fringes of *E. dukesi calhouni* are mostly dark and match the dorsal ground color, but tend to become lighter in the anal region of the hindwing. In *E. d. dukesi,* the fringes are conspicuously lighter than the ground color.

Based on the limited material examined to date, there is essentially no evidence of intergradation between these two subspecies, and the level of differentiation suggests that the two taxa have been isolated for some time. The only *Euphyes d. dukesi* known to me from Georgia (Figs. 19–20) shows none of the pattern elements that characterize *E. d. calhouni.* The only specimen with unusual patterning is a single female *E. d. calhouni* from Seminole County, Florida, in which the two dorsal yellowish spots in the discal region of the forewing are present but very faint—there is no evidence of these spots ventrally.

BIOLOGICAL AND DISTRIBUTIONAL NOTES

The recognition of *Euphyes dukesi calhouni* increases to five the number of *Euphyes* that are restricted to the southern coastal plain of eastern North America. A summary of the ecology of *Euphyes dukesi calhouni* is presented here; see Calhoun (1995) for a more extensive account.

The life history of *Euphyes d. calhouni* is similar to that of *E. d. dukesi* throughout its range (Mather 1963, Opler & Krizek 1984, Iftner, Shuey & Calhoun 1992, Calhoun 1995). The hostplants in central Florida are the sedges, *Rhynchospora inundata, R. miliacea* (Lam.) and an unidentified *Carex* species (Cyperaceae) (Calhoun 1995). Females have been observed ovipositing on these sedges, and pupal exuviae have been found attached to them. As in most *Euphyes,* other sedge species which grow in appropriate habitats are probably exploited as well.

Euphyes dukesi calhouni is a swamp inhabitant, preferring areas where its hostplant forms dense stands in small clearings (Calhoun 1995). Most of the known habitats that support this species are similar to the type locality. *Euphyes dukesi calhouni* has been observed feeding at the flowers of pickerelweed (*Pontederia cordata* L.), smartweed (*Polygonum punctatum* Elliot), and buttonbush (*Cephalanthus occidentalus* L.). Other butterflies found in these swamps include *Problema byssus* (Edwards), *Wallengrenia egeremet* (Scudder), *Cyllopsis gemma* (Hübner), and *Satyrodes appalachia* (Chermock). Interestingly, the habitat requirements and hostplants for *Satyrodes appalachia* in central Florida are nearly identical to those of *E. dukesi calhouni,* and they share both at several sites. The relationship noted between *S. appalachia* and *E. d. dukesi* in the Great Lakes region (Iftner, Shuey & Calhoun 1992) thus parallels that in central Florida with *E. dukesi calhouni.* As in the lower Great Lakes region, *S. appalachia* is the more tolerant species, occurring in several swamps that do not support *E. dukesi calhouni.*

Population densities vary from site to site. At Cabbage Swamp, *E. dukesi calhouni* is common, and several dozen individuals can be seen in the course of a day during peak emergence. However, at other nearby sites this skipper can be uncommon, and usually few adults are sighted. Low densities would appear to be the rule in northern Florida, given the rarity with which *E. dukesi calhouni* is collected.

There are two annual broods with no obvious phenotypic differences between them. Extreme dates of capture for the spring brood range from 9 May to 16 June. Extreme dates of capture for the summer brood ranged from 18 August to 13 October. There is a single record from July.

In flight, the adults appear dark and are reminiscent of large *Ancy-*

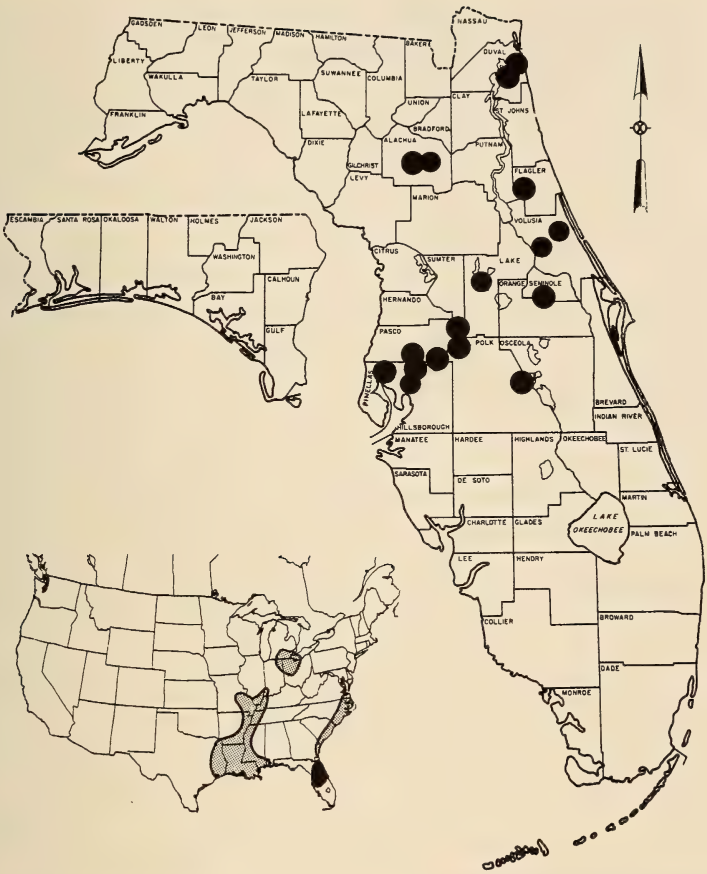


FIG. 23. The distribution of *Euphyes dukesi*. Solid dots and shading represent known localities and the generalized known range of *Euphyes dukesi calhouni*, new subspecies. Gray shading represents the generalized known range of *Euphyes dukesi dukesi*. Distributional data are derived from the material examined, Holmes et al. (1991) and from information provided by John V. Calhoun and Paul A. Opler.

loxpha numitor (Calhoun 1995). Like many wetland skippers, they are active under a variety of weather conditions ranging from sunshine to cloudy skies, and even to brief thunderstorms. Males often perch on blades of the hostplant in sunlit patches. Males also fly rapidly over and around patches of the hostplant (they occasionally fly slowly through the sedges, apparently in search of females). Females fly slowly and deliberately through the sedges, often at ground level. Males are more active and more readily observed than are females. Females are most often flushed from stands of the hostplant or found at flowers. Both sexes have been found in upland forests adjacent to Cabbage Swamp,

and one female was observed in a pasture at least 100 meters from the nearest suitable habitat (Calhoun 1995).

The number of known *E. dukesi calhouni* populations is at least 17, with over half of those discoveries coming since 1990 (see Calhoun 1995). Given that there were relatively few searches for populations prior to 1990, the increase in findings probably indicates that populations of *E. dukesi calhouni* are numerous. However, populations are quite localized and, given the intense pressure on wetlands from development in Florida, the species could be at risk if wetland alteration is not curtailed. Because populations of *E. dukesi calhouni* are localized and difficult to locate, and because the habitat is generally inhospitable to humans, I do not believe that limited collecting poses a significant threat to this taxon.

To date, *Euphyes dukesi calhouni* has been recorded only from peninsular Florida (Fig. 23). The known distributions of *Euphyes dukesi calhouni* and *E. d. dukesi* do not overlap—all specimens examined from Florida represent the new taxon, whereas all specimens from elsewhere are referable to *E. d. dukesi.* The two taxa approach each other in northeastern Florida and coastal Georgia, and in the material examined show virtually no intergradation. Additional field work and collecting along the eastern Georgia/Florida border and the Florida Panhandle would clarify potential distributional gaps, and help determine the status of populations in areas of potential sympatry.

The many morphologic differences between the two differentiates of *E. dukesi* in conjunction with the distribution and ecology of *E. dukesi calhouni* have convinced me that this taxon deserves at least subspecific status. The accumulation of so many differences between these two taxa suggests that they have been isolated for a considerable length of time and it is likely that they function as independent species if their ranges overlap. Thus, my decision to describe the Florida populations as a subspecies rather than as a full species is both conservative and arbitrary, and future investigations may well indicate that my decision is too conservative.

Most importantly, the recognition of *Euphyes dukesi calhouni* reveals yet another jewel in the collection of unique and highly endemic flora and fauna of Florida. This recognition increases the number of southern coastal plain restricted wetland *Euphyes* taxa to five, and adds another piece to the puzzle of wetland butterfly distribution and evolution in eastern North America.

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I am indebted to John V. Calhoun, who provided the bulk of the type series and all of the ecological and behavioral observations reported in this paper. The following institu-

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HESPERIIDAE OF CENTRAL RONDÔNIA BRAZIL: THREE NEW SPECIES OF *NARCOSIUS* (PYRGINAE)

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ABSTRACT. Three new species of *Narcosius* are described from western Brazil: *Narcosius steinhauseri, N. pseudomura,* and *N. odysseus. Narcosius pseudomura* was previously considered to have fallen within the normal range of variation of *N. mura.* A revised key to the males of the genus is presented.

Additional key words: *Narcosius colossus, N. hercules, N. nazaraeus, N. parisi, N. samson.*

Studies of butterflies in central Rondônia, Brazil, over the last several years (Emmel & Austin 1990, Austin et al. 1993) have revealed a number of new butterfly taxa (Austin 1993, Austin & Mielke 1993). Among these were three species of *Narcosius* (Hesperiidae: Pyrginae), a genus proposed and reviewed by Steinhauser (1986). Their discovery is not particularly surprising since several of the known taxa are quite rare in collections. Two of the new species apparently have not been taken elsewhere, while the third was previously considered to have fallen within the normal range of variation of a described species.

In the following descriptions, all forewing lengths are measured from the base to the apex. All measured specimens are from the Rondônia locality. Structures of the genitalia are those used by Steinhauser (1986).

Narcosius steinhauseri Austin, new species
(Figs. 1, 5)

Description. *Male.* Forewing length 30.3 mm (holotype) (range 28.5–32.0, n=10); forewing produced with prominent costal fold, termen evenly convex; hindwing termen evenly convex, slightly produced at tornus into pointed lobe; dorsal ground color dull black; wing bases glossy dark green proximal to hyaline macules on forewing, extending beyond end of discal cell posterior to M_1 and nearly to outer margin at tornus on hindwing, somewhat purplish in certain lights distad; forewing with white hyaline macules as follows: discal cell, nearly square, anterior edge slightly longer than posterior, variably excavate distad, slightly concave proximad; costal cell, relatively short, centered over discal cell macule (absent on one specimen); faint streak or none in Sc-R_1; CuA_1-CuA_2, the largest, more or less quadrate, posterior edge usually longer than anterior, excavate distad, slightly concave to straight proximad; M_3-CuA_1, small, triangular to rhomboidal, not reaching base of cell, completely overlapped by distal portion of macule in CuA_1-CuA_2; anterior portion of CuA_2–2A, variable, distal edge excavate or not, proximal edge straight, not overlapping macule in CuA_1-CuA_2, either contiguous with posterior-distal corner or disjunct; forewing fringe black, white in posterior half of CuA_2–2A; hindwing unmarked, fringe white to pale grayish with black at vein tips. Ventral surface dull black with indistinct gray overscaling, pure black at subapex and in discal cell, purplish towards paler anal margin which is pale brown basad; hyaline macules as on dorsum, that in Sc-R_1 larger, no extra white scaling adjacent to macule in CuA_2–2A; hindwing with relatively vague pattern created by sparse yellow and gray overscaling, gray concentrated on outer and anal margins, yellow largely basad and outlining postmedian area of ground color. Dorsal

head, thorax, and anterior abdomen gray-green, posterior abdomen dark greenish black with gray and, occasionally, red-brown at segments; palpi dark gray with numerous scattered white scales; pale gray beneath eyes, whiter behind; antennae black, some white on venter distad on shaft and on club, nudum gray to red-brown, 30 (n=2), 31 (n=2), or 32 (n=3) segments; ventral thorax gray becoming gray-green beneath wings, legs dark gray, mid and hind tibiae spined; ventral abdomen pale to dark gray, anal tuft white (n=15), mixed white and gray (n=3), or pale yellow (n=3). *Male genitalia.* Uncus divided with narrow arms relatively short, divergent; gnathos spiculose laterally; valva long, narrow, costa concave, ampulla long and narrowly curved over mesad, harpe long, dorsal margin with erect and moderately serrated triangular tooth, narrow caudal lobe of similar length, curved slightly ventrad, lightly serrated, sacculus more or less parallelogram-shaped; penis about length of valva, in lateral view relatively straight, caudal end not flattened, in dorsal view cephalic end rounded, not expanded, caudal edge curved, not dentate; cornutus a single long, slender spine. *Female.* Unknown.

Types. Holotype ♂ with the following labels: white, printed—BRASIL: Rondonia / 62 km S Ariquemes / linea C-20, 7 km E / B-65, Fazenda / Rancho Grande / 29 November 1991 / leg. G. T. Austin / (associated with / *Labidus praedator*); white, printed and hand-printed—Genitalic Vial / GTA—1611; red, printed—HOLOTYPE / *Narcosius steinhauseri* / Austin. Paratypes (all same location as holotype, leg. G. T. Austin unless otherwise noted; PL=at paper lures, EB=associated with *Eciton burchelli*): same data as holotype (1 ♂); 13 June 1993, EB, 1630–1700h (1 ♂); 14 June 1993, PL, 1500–1530h (1 ♂); 18 June 1993, PL, 1600–1630h (1 ♂); 13 August 1993, PL, 1530–1600h (1 ♂); 17 August 1993, EB, 1500–1530h (1 ♂); 20 August 1993, EB, 1600–1630h (1 ♂); 21 August 1993, EB, 1330–1400h (1 ♂); 6 October 1993, PL, 1200–1230h (1 ♂); 1430–1500h (1 ♂); 26 November 1991, EB (1 ♂); 11 November 1992, EB, 1400–1430h (1 ♂); 12 November 1992, EB, 1630–1700h (1 ♂); 14 November 1992, EB, 0930–1000h (1 ♂); 16 November 1992, EB, 1130–1200h (1 ♂); 18 November 1992, EB, 1600–1630h (1 ♂); 26 October 1992, leg. J. P. Brock, EB (2 ♂); 3 km E Fazenda Rancho Grande, lot 18, 25 September 1992 (1 ♂); 22 November 1992, leg. G. Bongiolo, PL, 1230–1300h (1 ♂). The holotype will be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil. The paratypes will be deposited in other collections.

Type locality. BRASIL: Rondônia; 62 km south of Ariquemes, linea C-20, 7 km (by road) east of route B-65, Fazenda Rancho Grande, 180 m. This is approximately 5 km northeast of Cacaulândia in typical lowland tropical rainforest. The types were taken while studying butterfly relationships with army ants (see Austin et al. 1993).

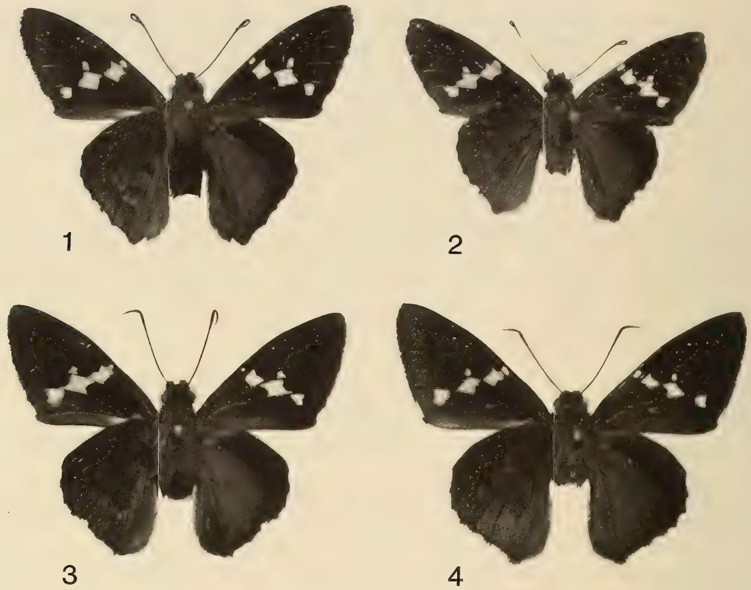
Etymology. It is a pleasure to name this species after my friend Stephen R. Steinhauser, who has added greatly to our knowledge of Neotropical skippers, including a revision of the *Narcosius,* and whose expertise has helped me in numerous ways.

Diagnosis and discussion. The superficial phenotypes of *Narcosius* are so similar that it is almost a necessity to examine the genitalia to determine species. The male genitalia of *N. steinhauseri* are readily distinguishable from described species. In Steinhauser (1986), this taxon initially keys to the second group with a "prominently rough or heavily spiculose" gnathos, then to those without a dorsal process on the ampulla, and finally to those with a dorsal projection on the harpe. From there, it is not included in the given options. The terminal end of the harpe has a pair of projections oriented at nearly right angles to each other, one directed caudad and the other dorsad, somewhat reminiscent of the harpe of *Astraptes aulus* (Plötz). These projections are prominently dentate on the facing edges. No other known *Narcosius* has a configuration of the harpe remotely resembling this. This species is known only from the type locality with records for June and August through November.

Narcosius pseudomura Austin, new species
(Figs. 2, 8)

Narcosius mura (Williams 1927), (Steinhauser 1986, in part)

Description. *Male.* Forewing length 32.0 mm (holotype), 31.1, 32.0 (paratypes); forewing produced and broadly convex with relatively long and narrow costal fold; hindwing



FIGS. 1–4. **1.** *Narcosius steinhauseri,* holotype male. **2.** *Narcosius pseudomura,* holotype male. **3.** *Narcosius mura,* male (BRAZIL: Rondônia; 62 km S Ariquemes, linea C-20, 7 km E B-65, Fazenda Rancho Grande). **4.** *Narcosius odysseus,* holotype male. On all figures, venter on left, dorsum on right.

termen slightly crenulate but evenly convex; dorsal ground color dull black; wing bases glossy dark green proximal to hyaline macules on forewing, extending beyond end of discal cell posterior to M_1 and nearly to outer margin at tornus on hindwing; forewing with white hyaline macules as follows: discal cell, nearly square, edges about equal, variably excavate distad, less so or slightly concave proximad; costal cell, small to minute, over proximal portion of discal cell macule; no macule in Sc-R_1; CuA_1-CuA_2, the largest, more or less quadrate, posterior edge longer than anterior, margin S-shaped distad, concave proximad; M_3-CuA_1, small, more or less quadrate, not reaching base of cell, partially overlapped by distal portion of macule in CuA_1-CuA_2; anterior portion of CuA_2–2A, variable, triangular to rhomboidal, distal edge excavate, proximal edge straight, contiguous with or slightly overlapping macule in CuA_1-CuA_2; forewing fringe black, white in posterior half of CuA_2–2A; hindwing unmarked, fringe white with black at vein tips. Ventral surface dull black with indistinct gray overscaling, pure black at subapex and in discal cell, purplish towards paler anal margin which is pale brown basad; hyaline macules as on dorsum, costal macule longer, streak present in Sc-R_1, macule in CuA_2–2A extended somewhat with white scaling caudad; hindwing dull greenish black with scattered pale yellow scales distad, no discernable pattern. Dorsal head, thorax, and anterior abdomen gray-green, posterior abdomen dark greenish black; palpi dark gray with numerous scattered white scales; gray beneath eyes, outlined with white, white behind; antennae black, apiculus gray, nudum dark red-brown, 30 (n=2) or 32 (n=1) segments; ventral thorax gray becoming gray-green beneath wings, legs gray, mid and hind tibiae spined; ventral abdomen charcoal gray, anal tuft white. *Male genitalia.* Uncus divided with moderately long, stout, and slightly divergent arms; gnathos with spiculose lobes; valva broad, costa relatively straight; ampulla narrowly curved over mesad, narrowly and deeply separated from harpe; harpe short, angled to broad and coarsely serrated tooth cephalad, serrations continued ventrad along cephalic margin facing ampulla; sacculus broad cephalad, angled

gradually caudad; penis somewhat longer than valva, evenly curved (concave ventrad in lateral view); short caudal medial projection in dorsal view, not dentate; cornutus a single long, slender spine. *Female.* Unknown.

Types. Holotype ♂ with the following labels: white, printed—BRASIL: Rondonia / 62 km S Ariquemes / linea C-20, 7 km E / B-65, Fazenda / Rancho Grande / 19 November 1991 / leg. D. Russell; white, printed and handprinted—Genitalic Vial / GTA—2284; red, printed—HOLOTYPE / *Narcosius pseudomura* Austin. Paratypes: ♂, same location as holotype, 5 December 1991, leg. G. T. Austin, associated with *Eciton burchelli*; ♂, 28 October 1992, leg. J. P. Brock, associated with *Eciton burchelli.* The holotype will be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil. The paratypes will be deposited in other collections.

Type locality. BRASIL: Rondônia; 62 km south of Ariquemes, linea C-20, 7 km (by road) east of route B-65, Fazenda Rancho Grande, 180 m. This is approximately 5 km northeast of Cacaulândia in typical lowland tropical rainforest.

Etymology. This species' name reflects its previous confusion with *Narcosius mura.*

Diagnosis and discussion. Steinhauser (1986) included *N. pseudomura* in his concept of *N. mura.* The variation which was noted within his concept of *N. mura* is largely accounted for by the present separation of the latter into two species. He illustrated the male genitalia of *N. pseudomura* as *N. mura.* The genitalia of *N. mura* (Fig. 7, see also Williams 1927) are similar to those of *N. pseudomura* but differ as follows: the ampulla is more broadly curved over mesad, the ampulla is more broadly and less deeply separated from the harpe, the harpe is shorter with its row of serrations shorter, the tooth of the harpe has no serrations on its cephalic margin facing the ampulla, and the penis is slightly shorter than the valva with its caudal margin more evenly curved in dorsal view. The holotype of *N. mura* illustrated by Williams (1927) and Steinhauser (1986) is nearly identical to specimens (Fig. 3) from the same locality as the types of *N. pseudomura.* These *N. mura* differ superficially from *N. pseudomura* as follows: they are somewhat smaller in size, the costal fold is shorter and broader, the macules are smaller and well separated, the hindwing margin has a slight lobe at vein 2A, the ventral hindwing has a relatively heavy yellowish overscaling which creates a discernable pattern where absent, the mid tibiae are not spined, and there are no white scales adjacent to the hyaline macule in cell CuA_2–2A on the ventral forewing. This species is known from the type locality with records between late October and early December and from Pará, Brazil.

Narcosius odysseus Austin, new species
(Figs. 4, 6)

Description. *Male.* Forewing length 27.2 mm (holotype); forewing termen broadly and evenly rounded with prominent costal fold; hindwing convex anteriorly, slightly concave posteriorly to short tornal lobe; dorsal ground color dull black; wing bases glossy dark green proximal to hyaline macules on forewing, extending beyond end of discal cell posterior to M1 and nearly to outer margin at tornus on hindwing; forewing with white hyaline macules as follows: discal cell, nearly square, anterior edge slightly longer than posterior, excavate distad, slightly concave proximad; costal cell, relatively short, centered over discal cell macule; faint dot in Sc-R_1; CuA_1-CuA_2, the largest, more or less hourglass-shaped, posterior edge longer than anterior, deeply excavate distad, less so proximad; M_3-CuA_1, small, quadrate, not reaching base of cell, completely overlapped by distal portion of macule in CuA_1-CuA_2; anterior portion of CuA_2–2A, more or less rhomboidal, distal edge slightly excavate, proximal edge slightly concave, contiguous with macule in CuA_1-CuA_2; forewing fringe black, white in posterior half of CuA_2–2A; hindwing unmarked, fringe white to gray basad, white distad with black at vein tips. Ventral surface dull black, forewing brownish purple towards paler anal margin which is pale brown basad; hyaline macules as on dorsum, that in Sc-R_1 as long as costal macule, macule in CuA_2–2A with some additional white scaling basad; hindwing with very sparse pale yellow overscaling, no discernable pattern. Dorsal head, thorax, and anterior abdomen gray-green, posterior abdomen dark greenish black with gray at segments; palpi dark gray with numerous scattered white scales; white beneath and behind eyes; antennae black, some white on venter and

beneath club, nudum gray, 24 segments; ventral thorax gray-brown becoming gray-green beneath wings, legs gray-brown, mid and hind tibiae spined; ventral abdomen charcoal gray, anal tuft gray with a few white scales. *Male genitalia.* Uncus divided with long, narrow arms, these wide apart in ventral view; gnathos very weakly spiculose; valva broad, stout; ampulla short, curved over mesad; harpe short, broadly triangular, slightly produced cephalad, dorsal margin finely serrate; sacculus short, roughly triangular; penis very slightly shorter than valva, slightly concave ventrally in lateral view, cephalic end broad, somewhat expanded laterally in dorsal view, caudal end flat in lateral view, squared in dorsal view, left side with fine teeth caudad. *Female.* Unknown.

Types. Holotype ♂ with the following labels: white, printed and handprinted—BRASIL, Rondonia, / 62 km S Ariquemes / linea C-20, 7 km E B-65, / Fazenda Rancho Grande / leg. Jim P. Brock / 28 Oct 1992 / assoc w/ *E. burchelli* / 1:00–1:30 [=1300–1330h]; white, printed and handprinted—Genitalic Vial / GTA—3197; red, printed—HOLOTYPE / *Narcosius odysseus* / Austin. The holotype will be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil.

Type locality. BRASIL: Rondônia; 62 km south of Ariquemes, linea C-20, 7 km (by road) east of route B-65, Fazenda Rancho Grande, 180 m. This is approximately 5 km northeast of Cacaulândia in typical lowland tropical rainforest.

Etymology. The species is named after the king of Ithaca in Greek mythology.

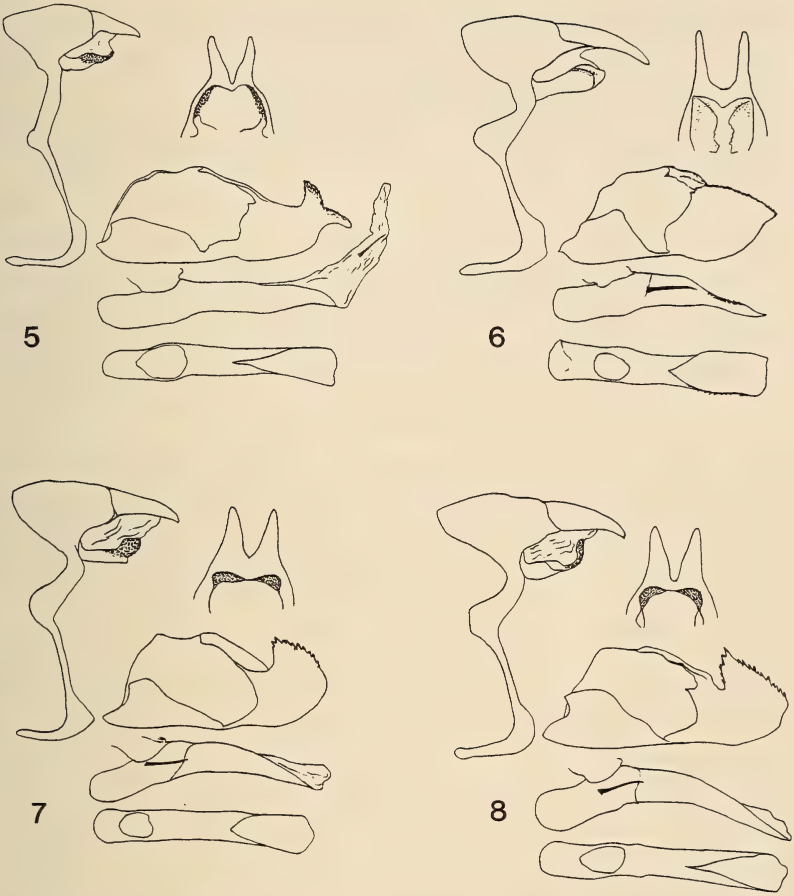
Diagnosis and discussion. This is a small *Narcosius* but otherwise similar in color and pattern to the other species in the genus. The male genitalia are most like those of *N. parisi* (Williams 1927). The smooth gnathos is similar to that species in form as is the relatively long uncus and spatulate penis. The valva differs from those of all known species by having little modification of either the harpe or the ampulla. The species is known only from the holotype taken in late October.

These three newly described *Narcosius* species fly with six additional congeners at their type locality: *N. parisi parisi, N. hercules* (Bell), *N. mura, N. colossus granadensis* (Möschler), *N. nazaraeus* Steinhauser 1986, and *N. samson* (Evans). Of the remaining three known species, *N. narcosius* (Stoll) may also occur in central Rondônia. It has been recorded in Bolivia, Peru, and Brazil; *N. aulina* (Evans) is known only from northern South America and *N. dosula* (Evans) occurs in southernmost Brazil (see Evans 1952, Steinhauser 1986). With nine of the twelve described species present, Rondônia appears to be the center of diversity for the genus.

With three new species now known for the genus, Steinhauser's (1986) key to the males needs modification. The following key is only to species; subspecific determinations may be made from the original key:

Key to the species of male *Narcosius*

1. Gnathos sclerotized but smooth or only lightly spiculose 2
1′. Gnathos sclerotized, prominently rough or heavily spiculose 4
2. Harpe without dorsal process . . . . *odysseus*
2′. Harpe with dorsal process 3
3. Dorsal process of harpe from near distal end, a simple long spine projecting dorsad, variously dentate . . . . *parisi*
3′. Dorsal process of harpe from near center of harpe, projecting fore and aft parallel to dorsal margin, dentate . . . . *hercules*
4. Ampulla with prominent dorsal process, harpe terminally pointed, penis with curved single row of very prominent teeth on left side extending distally to ventral side of terminus 5



FIGS. 5–8. **5.** *Narcosius steinhauseri,* holotype male genitalia, vesica partially extruded. **6.** *Narcosius odysseus,* holotype male genitalia, vesica not extruded. **7.** *Narcosius mura,* male genitalia (GTA-3192, BRAZIL: Rondônia; Fazenda Rancho Grande), vesica not extruded. **8.** *Narcosius pseudomura,* paratype male genitalia (GTA-3191), vesica not extruded. Shown in all figures are: lateral view of tegumen, gnathos, uncus, and associated structures; ventral view of uncus, gnathos, and anterior tegumen; interior of right valva; left lateral view of penis; and dorsal view of penis (latter without vesica and cornutus).

4′. Ampulla without dorsal process, harpe not terminally pointed, penis with scattered fine teeth on left side distally or may be smooth 6
5. Dorsal process of ampulla more or less circular, not projecting very far caudad . . . . *samson*
5′. Dorsal process of ampulla more or less rhomboid, projecting prominently caudad . . . . *nazaraeus*
6. Distal end of harpe with both dorsal and caudal projections . . . . *steinhauseri*
6′. Distal end of harpe without caudal projection 7
7. Terminally rounded harpe not prominently produced dorsad, dentate along its entire dorsal edge . . . . *narcosius*

7′. Terminally rounded harpe prominently produced dorsad, dentate only on produced portion 8
8. Harpe with additional dorsal process near its juncture with ampulla . . . . . . *aulina*
8′. Harpe produced dorsad only at distal end 9
9. Terminal portion of harpe prominently recurved, projecting cephalad, dentation very coarse and prominent . . . . *dosula*
9′. Terminal portion of harpe may be very coarsely dentate, but not recurved cephalad 10
10. Harpe long and slender . . . . *colossus*
10′. Harpe not long and slender 11
11. Ampulla broadly curved over mesad, harpe broadly and shallowly separated from ampulla, dorsal projection of harpe relatively short, penis slightly shorter than valva, VFW with no opaque white associated with macule in CuA_2–2A . . . . *mura*
11′. Ampulla narrowly curved over mesad, harpe narrowly and deeply separated from ampulla, dorsal projection of harpe relatively long, penis longer than valva, VFW with opaque white associated with macule in CuA_2–2A . . . . . *pseudomura*

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BUTTERFLIES OF THE JEMEZ MOUNTAINS OF NORTHERN NEW MEXICO

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ABSTRACT. We present capture records for 155 species of butterflies taken in the Jemez Mountains of northern New Mexico. Emphasis is on the authors' experiences during 1983–1985, and on the old Woodgate collection assembled during 1912–1913.

Additional key words: John Woodgate, faunal survey, checklist.

This paper is the fifth in a series treating the butterfly faunas of the major mountain ranges in New Mexico except the San Juans and Sangre de Cristos, which are unbroken extensions of the Colorado Rockies. The first (Holland 1974) dealt with the six ranges in the central part of the state. The second (Ferris 1976, 1977) reported on the Grant-Catron County area, including the extensive Gila Mountains complex. The third (Holland 1984) was devoted to the Zuni and Chuska Mountains of northwestern New Mexico and northeastern Arizona. The fourth (Cary 1994) reported on the Animas mountains in the extreme southwestern corner of New Mexico. The Animas Mountains are almost entirely on the Gray Ranch, the preservation and study of which is a major project of the Nature Conservancy and the Animas Foundation. Surveys of the butterflies of the Sacramento, Capitan, Organ, Guadalupe, and Franklin Mountains in south-central New Mexico and west Texas also have been completed, and these findings will be published in the future. There are several outlying ranges of the Gila Mountains complex which also are being investigated. These include the Gallo/Mangas, Black Range, and Datil Mountains.

Eight other limited regional lists of the New Mexican butterfly fauna also have appeared, including Williams (1914), Toliver (1971), Snow (1883, 1885), Cockerell (1899), and Hubbard (1965, 1977a, 1977b). Toliver (unpubl. 1978 manuscript) compiled records of every butterfly specimen taken in New Mexico prior to 1978; this work recently has been updated, and now is generally available (Toliver, Holland & Cary 1994). Also, a condensed version of this state-wide atlas, with species occurrence broken down by counties, is now in the literature (Cary & Holland 1994).

The present paper documents surveys of the Jemez Mountains, a range situated in north-central New Mexico and closely linked to the

San Juan Mountains of Colorado and bordering northern New Mexico (see Fig. 1–2), focusing on work conducted primarily from 1983 to 1985. An entire article is devoted to this single range because of the vastness and complexity of the Jemez compared to other New Mexico ranges: it hosts more species (n=155) than any other New Mexican mountain complex except the Gila (n=165).

CHARACTERISTICS OF THE JEMEZ MOUNTAINS

The Jemez Mountains are nearly entirely volcanic, although there are a few Triassic red Chinle sandstone outcroppings to the northeast around Abiquiu and to the southwest around Jemez Pueblo. The entire range surrounds a vast caldera, Valle Grande. The highest point, Chicoma Mountain (3540 m), has a false treeline and a huge fire climax meadow on the south face, with Douglas fir (*Pseudotsuga taxifolia*) flourishing to the crest on the north slope. There are no Lower Sonoran or Arctic-Alpine areas in the Jemez. May is the driest month, August is the wettest, and precipitation is largely dependent on altitude, ranging from 0.2 to 0.8 m annually. The Jemez flora includes ponderosa pine (*Pinus ponderosa*), Gambel oak (*Quercus gambelii*), grey oak (*Quercus grisea*), several species of *Juniperus* and *Yucca*, *Ceanothus fendleri*, several columbines (*Aquilegia* spp.), several *Penstemon* spp. and paintbrushes (*Castilleja* spp.), and a great assortment of *Eriogonum*. Additionally present are locust (*Robinia* spp.), kinnickinnick (*Arctostaphylos uva-ursi*), a diversity of violets (*Viola* spp.), aspen (*Populus tremuloides*), cottonwood (*Populus fremontii*), and willow (*Salix* ssp.). Missing flora include Upper Sonora walnut (*Juglans* sp.), *Agave*, and mesquite (*Prosopis* spp.).

Generally speaking, butterfly endemism at the species level is rare in the New Mexican mountains, and the Jemez are typical in this regard. With the possible exception of *Speyeria atlantis nikias* (Ehrmann), the Jemez Mountains lack endemics. Dispersal barriers, especially from the boreal habitats of the Colorado Rockies, are weak and probably no more than 10,000 years old. Boreal species from the north, lower desert species from along the Rio Grande to the south, and Great Basin species from the west all penetrate the Jemez (in the case of boreal species, it is not always clear which species are Pleistocene relicts and which are subsequent colonizers). Even a few Great Plains species, most notably *Atrytonopsis hianna turneri* Freeman, have isolated colonies in the Jemez (these are all in tiny 165 sq. mi. Los Alamos County, where most of the habitats, for military reasons, have never been disturbed).

HISTORICAL NOTES ON JEMEZ MOUNTAINS COLLECTORS

In 1912–1913, John Woodgate collected extensively in the Jemez Mountains. A partial list (96 species) of the Woodgate material was

documented subsequently by Williams (1914), and from this material he described *Hesperia woodgatei* (Williams). All the Woodgate records are simply recorded as "Jemez Mountains, 6400–7000 feet" in the Williams list. However, some of the listed species (e.g., *Oeneis chryxus* (Doubleday & Hew.)) indicate that Woodgate collected at times well above 7,000 feet. Woodgate was a fence rider for the ranchers in the area rather than a tourist, and his wanderings may have been truly extensive. How widely he traveled from the Indian Pueblo of Jemez or the hot springs resort at Jemez Springs can not be determined.

Not all of Woodgate's Jemez material was deposited in the Williams collection (which is now at the Carnegie Museum). We base this on the discovery of a Woodgate specimen of *Occidryas anicia alena* (Barnes & Benjamin) in the American Museum of Natural History (AMNH). The specimen, taken on 5 May 1913 in the Jemez, represents a taxon not on Williams' 1914 list (it does appear that all the species found by Woodgate in the Jemez during 1912–1913 are represented in recent collections; however, *Incisalia fotis* (Strecker), which he took in 1916, has not been recaptured).

Holland (1984) wrote that Woodgate gave up collecting and fence riding around 1913 due to failing eyesight, but that as recently as 1970 some of his material was under glass in a bar in Jemez Springs. We are pleased to report here that the specimens are at present still at the bar, and as of at least 1935, Woodgate was still collecting (it also has come to our attention that Woodgate collected in the Jemez Mountains at least as late as 1916). In 1935, in Louisiana, he took the type series of *Basilarchia archippus watsoni* (dos Passos 1938).

Skinner (1913) described *Pamphila margarita* from the Woodgate material taken near Jemez Springs. This name is now treated as an infrasubspecific form of *Atrytonopsis python* (W. H. Edwards). Also, the oldest *Hesperia woodgatei* specimens were taken not by Woodgate at the type locality in 1912–1913, but in 1899 by Townsend at Colonia Juarez, Chihuahua, Mexico (Clench 1965). These specimens were sent to W. J. Holland at the Carnegie Museum, who did not discern anything unique about a *Hesperia* with antennae nearly as long as the forewing, although he did name an accompanying bright blue *Speyeria* from the same Chihuahua site (*S. nokomis coerulescens* (W. J. Holland)). Thus, *H. woodgatei* remained undescribed for fourteen additional years.

LOCALITIES

Specific collecting sites and their alphanumeric codes are given below. The locality symbols appear on the maps in Figures 1 and 2. The style of data presentation follows Ferris (1976).

FIG. 1. Jemez Mountains, New Mexico, collecting sites (northern portion) and 8000' elevation contour. Same scale as Fig. 2.

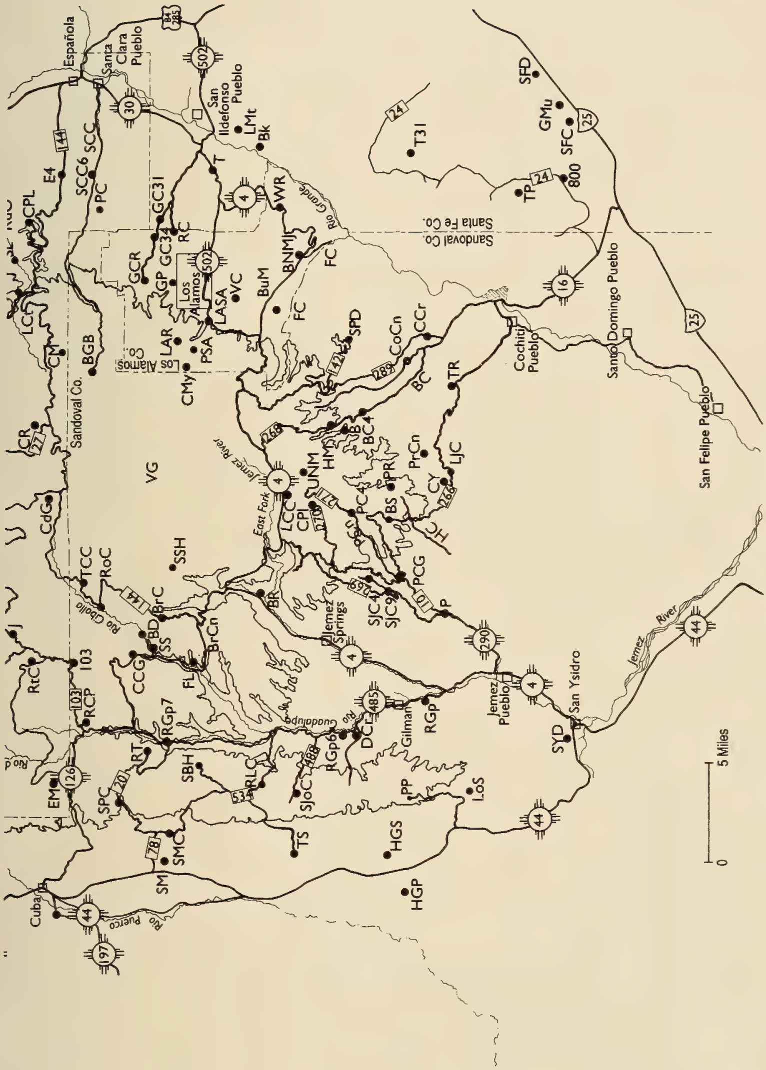

FIG. 2. Jemez Mountains, New Mexico, collecting sites (southern portion) and 8000' elevation contour. Same scale as Fig. 1.

JEMEZ MTS., LOS ALAMOS COUNTY, NEW MEXICO. Bandelier National Monument Junction, 6800' (2090 m) (**BNMJ**); Burnt Mesa, ca. 7300' (2250 m) (**BuM**); Camp May, 9800' (3020 m) (**CMy**); T.20N.R6E, Sec. 34, Guaje Canyon, 7000' (2160 m) (**GC34**); road end, Guaje Canyon Reservoir, 8000' (2460 m) (**GCR**); Los Alamos, Guaje Pines Cemetery, 7200' (2220 m) (**GP**); Los Alamos Reservoir, 8000' (2460 m) (**LAR**); 3 mi. below Los Alamos Ski Area, 8000' (2460 m) (**LASA**); Los Alamos (Pajarito) Ski Area, 10,000' (3080 m) (**PSA**); Los Alamos, Rendija Canyon, 7000' (2160 m) (**RC**); Valle Canyon, ca. 7500' (2300 m) (**VC**); White Rock, 6400' (1970 m) (**WR**).

JEMEZ MTS., RIO ARRIBA COUNTY, NEW MEXICO. Abiquiu, 5900' (1810 m) (**A**); Abiquiu Dam, 6500' (2000 m) (**AD**); SE corner, Abiquiu Grant, USFS Road 31 at USFS Road 418, 8000' (2460 m) (**AG**); Agua Sarca, near Mesa Puleo, 8000' (2460 m) (**AS**); Bear Spring, Cañada Gurule, 9000' (2770 m) (**Br**); Cañones Canyon, 6000' (1850 m) (**CC**); Cerro del Grant, 10,100' (3100 m) (**CdG**); summit, Chicoma Mt., 11,500' (3540 m) (**CM**); Cerro Pelon, 8500' (2620 m) (**CP**); Clara Peak Lookout, 8500' (2620 m) (**CPL**); Redondo Cienega, 10,100' (3100 m) (**CR**); T.21N.R4E, Sec. 2, Cañoncito Seco, 9000' (2770 m) (**CSc**); Mesa Gurule, Cañada Schmidt at USFS Road 77, 8000' (2460 m) (**CSt**); Cañon de Los Corrales, Corral Tank, 8000' (2460 m) (**CT**); 5 mi. S of Coyote, Coyote Canyon, 7700' (2370 m) (**CyCn**); Deadman's Crossover, 8500' (2620 m) (**DC**); Deadman Lookout, 8800' (2710 m) (**DLO**); Desert Monastery, 6500' (2000 m) (**DM**); radio towers, Eureka Mesa, 9900' (3050 m) (**EM**); Encino Point Lookout, 9900' (3050 m) (**EPL**); below El Vado Dam, 7000' (2160 m) (**EVD**); 4 mi. W of Española on USFS Road 144, 6400' (1970 m) (**E4**); USFS Road 8, French Mesa at Guadalupita Tank, 8000' (2460 m) (**GlT**); T.25N.R2E, Sec. 23, Golondrino Mesa, 8000' (2460 m) (**GM**); Gallina Peak, 8900' (2740 m) (**GPk**); T.25N.R2E, Sec. 9, Golondrino Tank, 8000' (2460 m) (**GT**); Jarosa, 8500' (2620 m) (**J**); 21 mi. W of Espanola, USFS Road 144 at Rio del Oso, La Cieneguita, 8000' (2460 m) (**LCt**); T.24N.R2E, Sec. 32, La Jara Tank, Mesa Cañada, 8200' (2530 m) (**LJT**); T.22N.R4E, Sec. 1, La Mesa del Pedregosa, 9200' (2830 m) (**LMP**); electronics site, Lobato Mesa, 9000' (2770 m) (**LoM**); La Sotella, 9000' (2770 m) (**LS**); Mine Canyon at Rio Chama, 6500' (2000 m) (**MC**); USFS Road 64, T.24N.R2E, Sec. 32, Mesa Cañada, 8500' (2620 m) (**MCd**); USFS Road 77 at Mesa Corral, 8000' (2460 m) (**MCr**); Mesa Gurule, 8000' (2460 m) (**MG**); 1 mi. E of Junction of NM Hwy 112 and NM Hwy 96, 7500' (2310 m) (**NMJ1**); T.21N.R2E, Sec. 5, N slope of Jemez Mts., North Rio Puerco, 9200' (2830 m) (**NRP**); Puye Cliffs, 7000' (2160 m) (**PC**); Poleo Creek, 8000' (2460 m) (**PCr**); T.22N.R5E, Sec. 17, Polvadera Creek, 8000' (2460 m) (**PrCr**); Resumidero, 9000' (2770 m) (**R**); Rio Puerco Campground, 8500' (2620 m) (**RCG**); 8 mi. up Rio del Oso from US Hwy 84, 6400' (1970 m) (**RdO**); T.21N.R2E, Sec. 27, Rito Cafe, 9000' (2770 m) (**RtC**); Rio del Oso at San Lorenzo, 7400' (2280 m) (**SL**); Mine Canyon at Sargent Tank, 8000' (2460 m) (**ST**); San Pedro Parks Wilderness, 9000'-10,500' (2770–3230 m) (**SPP**); Tusas Cañada at Mesa Alta, USFS Road 77, 8000' (2460 m) (**TC**); Mesa Gurule, Tank in T.28N.R2E, Sec. 18, 8500' (2620 m) (**T18**); Valle de La Grulla, 9800' (3020 m) (**VLG**); USFS Road 8 at Wildhorse Tank, Rio Gallinas Valley, 7500' (2310 m) (**WHT**); USFS Road 77, 0.5 mi. N of NM Hwy 96 near Gallina, 8000' (2460 m) (**77**).

JEMEZ MTS., SANDOVAL COUNTY, NEW MEXICO. Bland, 7500' (2310 m) (**B**); Bland Canyon, 7000' (2160 m) (**BC**); 4 mi. up Bland Canyon from Natl. Forest boundary, 6500' (2000 m) (**BC4**); Beaver Dam near Seven Springs, 8200' (2530 m) (**BD**); Santa Clara Canyon at Baca Land Grant boundary, 9000' (2770 m) (**BGB**); Bear Paw Lake, Regina, 7500' (2310 m) (**BPL**); Battleship Rock, 7000' (2160 m) (**BR**); USFS Road 144 at Bear Canyon, 8500' (2620 m) (**BrC**); Barley Canyon, 8200' (2520 m) (**BrCn**); Bear Spring, 8000' (2460 m) (**BS**); Calaveras Campground, 8000' (2460 m) (**CCG**); 1.5 mi. S of Natl. Forest boundary, Dome Lookout Road at Cochiti Creek, 5600' (1720 m) (**CCr**); Cochiti Canyon, 5900' (1820 m) (**CoCn**); Cerro Pelado, 10,000' (3080 m) (**CPl**); Cerrito Yelo, 7500' (2310 m) (**CY**); Guadalupe River at Deer Creek, 6800' (2090 m) (**DCr**); Frijoles Canyon, Bandelier Natl. Monument, 6000' (1850 m) (**FC**); Fenton Lake, 7800' (2400 m) (**FL**); T.17N.R4E, Sec. 18, Hondo Canyon, 8000' (2460 m) (**HC**); Holy Ghost Pond, 6400' (1970 m) (**HGP**); Holy Ghost Springs, 6600' (2030 m) (**HGS**); Horn Mesa, 1 mi. N of Bland, 7500' (2310 m) (**HM**); Los Conchas Campground, 8400' (2590 m) (**LCC**); ca. 13 mi. NW of Cochiti Pueblo, La Jara Corral and La Jara Creek (but not La

Jara Tank, which is in Rio Arriba Co.), 7000' (2160 m) (**LJC**); road up Pajarito Peak, Log Spring, 8000' (2460 m) (**LoS**); 7 mi. N of junction with NM Hwy 44 on NM Hwy 96, 7600' (2340 m) (**NMJ2**); Ponderosa, 6000' (1850 m) (**P**); Paliza Campground, 7200' (2220 m) (**PCG**); Paliza Canyon, 7800' (2400 m) (**PCn**); 4 mi. N of Paliza Campground in Paliza Canyon, 7800' (2400 m) (**PC4**); Pajarito Peak, 9000' (2770 m) (**PP**); 4 mi. from NM Hwy 44 up road to Pajarito Peak, 8000' (2460 m) (**PP4**); 6 mi. NE of Paliza Campground at Peralta Ridge, 8800' (2460 m) (**PR**); Peralta Canyon, 7000' (2160 m) (**PrCn**); USFS Road 144 at Road Canyon, 8500' (2620 m) (**RoC**); Rock Creek Park, 9300' (2860 m) (**RCP**); Rio Guadalupe, 0.5 mi. NW of NM Hwy 4 near Gilman, 5800' (1790 m) (**RGp**); Rio Guadalupe, 6 mi. upstream from NM Hwy 4, 6500' (2000 m) (**RGp6**); Rio Guadalupe, 7 mi. downstream from NM Hwy 126, 7700' (2370 m) (**RGp7**); T.19N.R1E, Sec. 33, Rito La Cueva, 8400' (2590 m) (**RLC**); Red Top, 9100' (2800 m) (**RT**); Smokey Bear Hill, 8400' (2590 m) (**SBH**); Santa Clara Canyon, 6200' (1910 m) (**SCC**); 6 mi. up Santa Clara Canyon from Española, 6800' (2090 m) (**SCC6**); T.17N.R3E, Sec. 4, San Juan Canyon, 6800' (2090 m) (**SJC4**); T.17N.R3E, Sec. 9, San Juan Canyon, 6600' (2030 m) (**SJC9**); summit, San Joaquin Canyon, 8400' (2590) (**SJoC**); San Jose Canyon, 8000'-8500' (2460–2620 m) (**SJsC**); San Miguel, 7000' (2160 m) (**SM**); San Miguel Canyon at Natl. Forest boundary, 7200' (2220 m) (**SMC**); San Pablo Canyon, 5 mi. W of Red Top, 8000' (2460 m) (**SPC**); Dome Lookout at St. Peter's Dome, 8800' (2710 m) (**SPD**); Seven Springs Fish Hatchery, 8000' (2460 m) (**SS**); Sulphur Springs Hotel (ruins), 8800' (2710 m) (**SSH**); San Ysidro dump, 5400' (1660 m) (**SYD**); Pipeline Road at Twin Cabins Canyon, 8500' (2620 m) (**TCC**); Tent Rocks near Cochiti Pueblo, 5500' (1690 m) (**TR**); 2.5 mi. W of crest of Sierra Nacimiento, E of Thompson Spring, 7800' (2400 m) (**TS**); UNM Biology Cabin, ca. 8000' (2460 m) (**UNM**); Valle Grande, 8500'-10,000' (2620–3080 m) (**VG**), 5 mi. E of NM Hwy 126 on Pipeline Road, 9000' (2770 m) (**103**).

JEMEZ MTS., SANTA FE COUNTY, NEW MEXICO. Rio Grande, 1 mi. S of Buckman, 5300' (1630 m) (**Bk**); T.20N.R7E, Sec. 31, Guaje Canyon, 6500' (2000 m) (**GC31**); Golondrinas Museum, 5800' (1790 m) (**GMu**); 3 mi. S of San Ildefonso Pueblo, La Mesita, 5600' (1720 m) (**LMt**); La Cienega, Santa Fe Canyon, 5600' (1720 m) (**SFC**); Santa Fe Downs, 7000' (2160 m) (**SFD**); Totavi, 6000' (1850 m) (**T**); Tetilla Peak, 7000' (2160 m) (**TP**); west of Santa Fe, T.17N.R7E, Sec. 3, Tank in 31 Draw, 6500' (2000 m) (**T31**); La Bajada Mesa, 800 Well, 6000' (1850 m) (**800**).

CHECKLIST

In the following checklist, counties, flight periods, and elevation ranges are noted. A plus (+) before a date indicates a common species that flies considerably later than the date indicated, but for which late-season specimens were merely observed, not collected. Nomenclature and species number follows Miller and Brown (1981) as amended by Ferris (1989), except in a few cases where our opinion is different.

Collectors who have supplied records include Ray Stanford (RES), James A. Scott (JAS), Glenn Scott (GS), Michael Toliver (MT), Robert Langston (RL), Oakley Shields (OS), Scott Ellis (SLE), Cliff Ferris (CDF), Richard A. Bailowitz (RAB), Dorothy Hurd (DH), and Carl Cushing (CC). Woodgate records from the old Williams list are denoted by (W). Other Woodgate records are indicated by (JW). Most of the Williams collection is currently at the Carnegie Museum, although some specimens may be at the American Museum of Natural History. In general, Woodgate's other Jemez Mountains material may be found at major museums throughout the country. We have not checked Euro-

pean museums, but we would not be surprised to find Jemez Mountains specimens collected by Woodgate there.

We are aware of some reports (mostly old) of species from the Jemez that we do not believe to be correct or possible. These reports, which have been purged from our list, include *Papilio indra* Reakirt, *Epidemia nivalis browni* (dos Passos), *Thorybes bathyllus* (J. E. Smith), *Erynnis martialis* (Scudder), *Amblyscirtes fimbriata* (Plotz), *Cyllopsis henshawi* (W. H. Edwards), *Charidryas palla calydon* (Holland), and *Apodemia mormo mejicana* (Behr). The last of these taxa may be possible from the eastern edge of the Jemez, although all Jemez *A. mormo* (C. & R. Felder) we have seen labeled *mejicana* are actually misdeterminations of typical *A. m. mormo* from the western portion of the Jemez.

HESPERIIDAE

7a. *Epargyreus clarus clarus* (Cramer). May 11 (W) to July 31, 6500' to 10,000'. **Los Alamos Co.**: LASA, VC(CC), BuM(SJC), CMy(SJC). **Rio Arriba Co.**: RCG(CC). **Sandoval Co.**: SPC, RLC, SSH, Guadalupe Canyon 1 mi. N of tunnels, 3 mi. up road to PP, (W, as *Eudamus tityrus* (Fabr.)).

20. *Zestusa dorus* (W. H. Edwards). April 16 to May 9, 6500' to 8500'. **Rio Arriba Co.**: 4 mi. N of El Rito (JAS). **Sandoval Co.**: SPD, BC4, BC(CC), (W).

48. *Thorybes pylades* (Scudder). May 7 to +June 30, 6500' to 10,000'. **Los Alamos Co.**: BuM(SJC). **Rio Arriba Co.**: 3 mi. E of CM, DLO, GMu. **Sandoval Co.**: BC4, SBH, 4 mi. E of Regina in SJsC, HC, (W).

50. *Thorybes mexicanus* (Herrich-Schaffer) complex. April 26 to July 31, 7800' to 10,000'. **Los Alamos Co.**: PSA, VC(CC), CMy(SJC), BuM(SJC). **Rio Arriba Co.**: LCt, 3 mi. E of CM, MCd. **Sandoval Co.**: RT, SBH, SSH, 10 mi. N of PCG, BGB, CPl, (W).

83. *Erynnis icelus* (Scudder & Burgess). May 6 to July 7, 6500' to 8400'. **Los Alamos Co.**: GCR, VC(CC). **Rio Arriba Co.**: EM(JAS). **Sandoval Co.**: BC4, SBH, PC4, (W).

84c. *Erynnis brizo burgessi* (Skinner). April 27(W) to July 3, 6200' to 8500'. **Los Alamos Co.**: VC(CC). **Rio Arriba Co.**: MCd, GPk(JAS). **Sandoval Co.**: SPD, CY, 5 mi. S of Jemez Springs, (W).

86. *Erynnis telemachus* Burns. April 20(W) to July 22, 6400' to 9000'. **Los Alamos Co.**: VC(CC). **Rio Arriba Co.**: CyCn, PrCr, RdO, MCd, 77, NM Hwy 112 at DLO turnoff. **Sandoval Co.**: 1 mi. up BC from BC4, PP4, DCr, PP, (W, as *Thanaos propertius* (Scudder & Burgess)).

88. *Erynnis meridianus* Bell. **Sandoval Co.**: Jemez Springs (Burns, 1964, specimen possibly mislabelled).

90. *Erynnis horatius* (Scudder & Burgess). April 22 to Aug. 26. **Rio Arriba Co.**: Arroyo de los Frijoles near A(SJC), Cañon de la Presa near Rio Chama (SJC). **Sandoval Co.**: FC(CC), (W).

93a. *Erynnis pacuvius pacuvius* (Lintner). April 22 to July 25, 7500' to 9200'. **Los Alamos Co.**: VC(CC), GC(CC). **Rio Arriba Co.** GPk(SJC), EM(JAS). **Sandoval Co.**: PP, RT, 4 mi. E of Regina in SJsC, SPD, 2.5 mi. up road to PP, (W).

95. *Erynnis funeralis* (Scudder & Burgess). June 13 to Aug. 30, 6800' to 7800'. **Los Alamos Co.**: GC34(CC). **Sandoval Co.**: PC4, SJC4, FC(CC).

98–99. *Erynnis afranius* (Lintner) and *persius* (Scudder) complex. April 25(W) to Sept. 10(W), 5500' to 10,000'. Careful examination has shown *E. afranius* to exist in the Jemez Mountains in Sandoval and Sante Fe counties; similarly, we are confident that *E. persius* exists in Rio Arriba and Sandoval counties. **Los Alamos Co.**: PSA, VC(CC), BuM(SJC), CMy(SJC). **Rio Arriba Co.**: LCt, AS, 1 mi. S of EVD(MT). **Sandoval Co.**: 1 mi. up BC from BC4, CCr, RGp, PP4, 4.5 mi NW of Cochiti

Pueblo, 4 mi. down BC from B, LoS, Jemez Springs, 5 mi. S of SPD, CY, CPl, (W). **Santa Fe Co.**: GC31.

102. *Pyrgus xanthus* W. H. Edwards. May 7 to June 26, 7800' to 9800'. **Los Alamos Co.**: VC(CC), CMy(SJC). **Rio Arriba Co.**: CT. **Sandoval Co.**: BGB, PC4, 1.5 mi. N of RLC on USFS Road 534, (W).
103. *Pyrgus scriptura* (Boisd.). July 20, 7500'. **Sandoval Co.**: "5 mi. E of La Jara" (AMNH coll.). There are several places named La Jara in the Jemez Mountains.
104. *Pyrgus communis* (Grote) and *albescens* Plotz complex.; April 20 to Oct. 10, 5500' to 10,000'. **Los Alamos Co.**: Los Alamos (CC), LAR(CC), CMy(SJC). **Rio Arriba Co.**: PrCr, 77, DM, MC. **Sandoval Co.**: 2 mi. N of B, FC, SSH, CCr, Gilman, (W, as *Pyrgus tessellata* (Scudder)). **Santa Fe Co.**: La Bajada (CC).
109. *Heliopetis ericetorum* (Boisd.). July 1, 6500'. **Rio Arriba Co.**: MC.
115. *Pholisora catullus* (Fabr.). May 19 to Aug. 19, 5600' to 7400'. **Sandoval Co.**: Rio Guadalupe at Rio de Las Vacas, (W). **Santa Fe Co.**: SFC.
118a. *Hesperopsis alpheus alpheus* (W. H. Edwards).; May 19 to Aug. 7, 5400' to 6500'. **Rio Arriba Co.**: NMJ1(JAS). **Sandoval Co.**: SYD, HGS.
121. *Piruna pirus* (W. H. Edwards). June 9 to July 30, 7000' to 10,000'. **Los Alamos Co.**: GC34. **Rio Arriba Co.**: 1 mi. S of LCt. **Sandoval Co.**: DCr, RLC, E side of VG, PC4, (W).
145. *Oarisma garita* (Reakirt). June 9 to July 31, 7000' to 9800'. **Los Alamos Co.**: GC34, 1 mi. N of GP, VC(CC), CMy(SJC). **Rio Arriba Co.**: VLG, RtC, 1.5 mi. N of DC, MCd, LJT. **Sandoval Co.**: RGp7, CCG, east side of VG, 6 mi. W of SPD, SSH, 17 mi. W of BNMJ, PC4, (W).
146. *Oarisma edwardsii* (Barnes). May 20 to Aug. 2, 6500' to 7200'. **Los Alamos Co.**: 1 mi. N of GP, BuM(SJC). **Rio Arriba Co.**: 4 mi. NE of Gallina (SJC). **Sandoval Co.**: FC(CC), (W). **Santa Fe Co.**: GC31.
152. *Polites rhesus* (W. H. Edwards).; May 20 to May 28, 6400' to 8000'. **Rio Arriba Co.**: AG, RdO. **Sandoval Co.**: 1 mi. E of SMC, CT, (W).
155. *Stinga morrisoni* (W. H. Edwards). April 21 to June 30(W), 8000' to 10,000'. **Los Alamos Co.**: Los Alamos (CC), VC(CC), BuM(SJC). **Rio Arriba Co.**: CP, PrCr. **Sandoval Co.**: PP, BC(CC), (W).
156a. *Hesperia uncas uncas* W. H. Edwards. June 2 to Sept. 5, 5600' to 9000'. **Los Alamos Co.**: LAR(SJC). **Rio Arriba Co.**: 10 mi. S of AD, 3 mi. S of AD, E4, 1 mi. SE of A, LoM, MC. **Sandoval Co.**: HGS, Gilman, 20 mi. S of Cuba on NM Hwy 44, (W). **Santa Fe Co.**: 800, T31, LMt.
157. *Hesperia juba* (Scudder). May 19(W) to Aug. 31, 6500' to 9100'. **Rio Arriba Co.**: AD, 77. **Sandoval Co.**: PP4, LoS, 2 mi. NE of PCG, BPL, summit E of TS, (W).
158l. *Hesperia comma colorado* (Scudder). July 31 to Sept. 20(W), 7000' to 9000'. **Los Alamos Co.**: 4 mi. W of Los Alamos (SJC). **Rio Arriba Co.**: AS, 4 mi. W of DLO, DLO, 1 mi. E of NMJ1, 77, 2 mi. N of Gallina on USFS Road 8, Br. **Sandoval Co.**: BPL, 1 mi. S of Regina, SPC(RES), (W).
159. *Hesperia woodgatei* (Williams). Aug. 30 to Oct. 10. 5900' to 8400'. **Los Alamos Co.**: "North part of Los Alamos Co." (CC). **Rio Arriba Co.**: CPL (SJC). **Sandoval Co.**: 13 mi. NW of Cochiti Pueblo near BS, SPD, PCn, CoCn, (W, type series).
163a. *Hesperia pahaska pahaska* (Leussler). May 28 to Sept. 15, 6000' to 10,000'. **Los Alamos Co.**: GC34. **Rio Arriba Co.**: AD, CP, E4. **Sandoval Co.**: PP, 4 mi. W of CCG, SM, CY, SPD, NM Hwy 44 at road to PP, NMJ2. **Santa Fe Co.**: TP, T31.
166. *Hesperia viridis* (W. H. Edwards). May 5 to Sept. 10, 5800' to 9000'. **Los Alamos Co.**: BuM(SJC & DH). **Rio Arriba Co.**: 2 mi. S of A, AD, LS, 2 mi. S of DM. **Sandoval Co.**: RGp, LoS, 4 mi. S of Jemez Springs, DCr, SCC6, PP, SM, 1 mi. N of Jemez Pueblo, NM Hwy 44 at road to PP. **Santa Fe Co.**: GC31, TP, LMt.
173. *Hesperia nevada* (Scudder). June 17 to July 28, 8300' to 9900'. **Los Alamos Co.**: CMy(SJC). **Rio Arriba Co.**: EPL(JAS). **Sandoval Co.**: LJC(JAS); 5 mi. E of Regina in SJsC.
175a. *Polites sabuleti sabuleti* (Boisd.). June 6(W) and Aug. 19, 5600'. **Sandoval Co.**: (W). **Santa Fe Co.** SFC.
177. *Polites draco* (W. H. Edwards). May 22 to July 16, 7800' to 11,500'. **Los Alamos**

Co. PSA(SJC), CMy(SJC). **Rio Arriba Co.**: CR, CM, CSc, MCr. **Sandoval Co.**: SBH, RLC, 2 mi. N of SSH, PC4, BGB, road up CPl, 10 mi. E of Cuba on NM Hwy 126.

179. *Polites themistocles* (Latreille). June 10 to July 31, 7700' to 10,100'. **Los Alamos Co.**: PSA, Los Alamos (CC), VC(CC), CMy(SJC). **Rio Arriba Co.**: CR, CSc, CSt, MCr. **Sandoval Co.**: RGp7, RLC, 2 mi. N of SSH, 17 mi. W of JBNM on NM Hwy 4, PC4, HC, NMJ2, (W, as *Pamphila cernes* (Boisd. & Leconte)).

187a. *Atalopedes campestris campestris* (Boisd.). July 31. **Sandoval Co.**: SSH (AMNH coll.). Probable in the Jemez, and there is no reason to question this record; if anything is curious, it is that this is the only record.

192c. *Ochlodes sylvanoides napa* (Boisd.). Aug. 12 to Sept. 1, 6800' to 9000'. **Rio Arriba Co.**: AS, 2 mi. N of Gallina on USFS Road 8, CSt, Br. **Sandoval Co.**: 1 mi. N of Regina.

194. *Paratrytone snowi* (W. H. Edwards). July 21 to Aug. 29, 7200' to 8000'. **Los Alamos Co.**: 4 mi. W of Los Alamos (SJC). **Sandoval Co.**: PC4, 3 mi. N of PCG, above SJC4 in Section 33.

199. *Poanes taxiles* (W. H. Edwards). June 16 to Aug. 13, 6200' to 10,000'. **Los Alamos Co.**: LASA, VC(CC), Los Alamos (CC), BuM(SJC). **Rio Arriba Co.**: DC, MC, 1 mi. S of EVD(MT). **Sandoval Co.**: 4 mi. down BC from B, PC4, Jemez Springs, (W).

217b. *Euphyes vestris kiowah* (Reakirt). May 24 to Aug. 22, 6000' to 8200'. **Los Alamos Co.**: GCR, VC(CC), BuM(SJC). **Rio Arriba Co.**: 10 mi. S of AD, PrCr, 1 mi. S of LCt, AS, GMu, 2 mi. below ST, near MC, 2 mi. S of DM. **Sandoval Co.**: 4 mi. down BC from B, 3 mi. N of PCG, RGp6, DCr, 2 mi. W of SPD, PC4, SM, (W). **Santa Fe Co.**: GC31.

219b. *Atrytonopsis hianna turneri* Freeman. May 30 to June 11, 7000' to 7600'. **Los Alamos Co.**: GC34, 1 mi. N of GP, BuM(SJC). **Sandoval Co.**: FC(CC).

222. *Atrytonopsis vierecki* (Skinner). May 13 to June 26(W), 5800' to 7200'. **Los Alamos Co.**: GC34, RoC, BuM(SJC). **Rio Arriba Co.**: AD. **Sandoval Co.**: SCC6, RGp, 2 mi. up road to PP, NM Hwy 44 at road to PP, (W). **Santa Fe Co.**: TP.

225. *Atrytonopsis python* (W. H. Edwards). May 15 to June 9(W), 5800' to 9200'. **Los Alamos Co.**: RoC. **Rio Arriba Co.**: 6 mi. E of CM, AD. **Sandoval Co.**: RGp, (W, as *Pamphila python* and as *Pamphila margarita* Skinner (the type series of *margarita*)).

228. *Amblyscirtes simius* W. H. Edwards. June 18 and July 30, 6300' to 6500'. **Los Alamos Co.**: GC34(CC). **Rio Arriba Co.**: E4. **Sandoval Co.**: 20 mi. S of Cuba on NM Hwy 44.

230. *Amblyscirtes cassus* W. H. Edwards. May 30(W) and June 17 to July 15, 7200' to 8000'. **Los Alamos Co.**: 1 mi. N of GP. **Rio Arriba Co.**: 1 mi. S of LCt. **Sandoval Co.**: PC4, (W).

231. *Amblyscirtes aenus* W. H. Edwards. May 17 to June 29, 6500' to 9200'. **Rio Arriba Co.**: 6 mi. E of CM. **Santa Fe Co.**: GC31. **Sandoval Co**: FC(CC), (W).

233. *Amblyscirtes oslari* (Skinner). May 15 to July 27, 5800' to 7600'. **Los Alamos Co.**: 1 mi. N of GP, Los Alamos (CC). **Rio Arriba Co.**: 1 mi. S of EVD(MT). **Sandoval Co.**: RGp, SCC6, Gilman, BC(CC), FC(CC). **Santa Fe Co**:. GC31.

244. *Amblyscirtes eos* (W. H. Edwards). June 20 and July 30, 5200' to 5600'. **Sandoval Co.**: Gilman, SYD, Jemez Springs (JW, specimen in AMNH; this species is not on Williams' 1914 list).

245. *Amblyscirtes vialis* (W. H. Edwards). May 13(W) to June 23, 7800' to 9000'. **Los Alamos Co.**: VC(CC). **Rio Arriba Co.**: 4 mi. NE of Gallina (SJC). **Sandoval Co.**: SBH, RLC, PC4, 103, (W).

249. *Amblyscirtes phylace* (W. H. Edwards). May 19 to July 4, 6400' to 8000'. **Los Alamos Co.**: VC(CC), BuM(SJC). **Rio Arriba Co.**: LCt, 2 mi. E of PC, MC. **Sandoval Co.**: 3 mi. E of Regina in SJsC, (W).

MEGATHYMIDAE

286a. *Megathymus coloradensis navajo* Skinner. April 12 to June 4(W), 6400' to 8000'. **Los Alamos Co.**: Los Alamos Canyon (CC). **Rio Arriba Co.**: RdO. **Sandoval Co.**: PP4, (W). **Santa Fe Co.**: SFD, GC31(SJC).

289a. *Megathymus streckeri streckeri* (Skinner). June 2–14, 6450' to 7000'. **Rio Arriba Co.**: 2 mi. E of PC, Rio Chama below DM(SJC).

PAPILIONIDAE

303a. *Papilio polyxenes asterius* Stoll. June 17 to Sept. 13(W), 9800' to 8900'. **Los Alamos Co.**: Los Alamos (CC), PSA(SJC), BuM(SJC). **Sandoval Co.**: SPD, 3 mi. up CPl spur road (USFS Road 270), near Clear Creek Campground (GS), 1 mi. S of Cochiti Dam (JAS), (W, as *Papilio polyxenes curvifascia* Skinner).

308. *Papilio bairdii* W. H. Edwards. May 19 to Aug. 28, 7600' to 10,000'. **Los Alamos Co.**: 1 mi. N of GP, Los Alamos (CC). **Rio Arriba Co.**: CP, CyCn, 3 mi. E of CM, CPL, 3 mi. S of A, PCr. **Sandoval Co.**: SPD, PP, FC(CC), (W). **Santa Fe Co.**: T(CC).

311a. *Papilio zelicaon zelicaon* Lucas. May 1(W) to July 9, 6200' to 10,000'. **Los Alamos Co.**: PSA(SJC). **Rio Arriba Co.**: 3 mi. E of CM, EM. **Sandoval Co.**: SPD, PP, RT, SPC, 4 mi. down BC from B, LJC, (W).

311b. *Papilio zelicaon* form "nitra" W. H. Edwards. May 2 to June 9, 7700' to 10,000'. **Rio Arriba Co.**: 3 mi. E of CM, CPL, CP, LS, 1 mi. N of GPk. **Sandoval Co.**: SPD.

321a. *Pterourus rutulus rutulus* Lucas. May 13(W) to Aug. 20, 6600' to 9800'. **Los Alamos Co.**: Los Alamos (CC), GC34(CC), CMy(SJC), BuM(SJC), VC(SJC). **Rio Arriba Co.**: RdO near SL, MG. **Sandoval Co.**: SCC6, SPC, PC4, HC, (W).

322. *Pterourus multicaudatus* (Kirby). May 6 to Sept. 19, 6200' to 9800'. **Los Alamos Co.**: Los Alamos (CC), WR(CC), VC(CC), BuM(SJC). **Rio Arriba Co.**: Rio Chama below DM(SJC). **Sandoval Co.**: 2 mi. up road to PP, SCC6, 4 mi. S of Jemez Springs, (W, as *Papilio daunus* Boisd.). **Santa Fe Co.**: Bk(CC), T(CC).

323. *Pterourus eurymedon* (Lucas). May 26(W) to July 7, 7200' to 10,000'. **Los Alamos Co.**: 1 mi. N of GP, Los Alamos (CC), PSA(SJC). **Rio Arriba Co.**: AS, PCr, 1.5 mi. N of DC, DLO, GPk(SJC). **Sandoval Co.**: USFS Road 652 near DCr, PP, 3 mi. N of PCG, (W).

PIERIDAE

329a. *Neophasia menapia menapia* (C. & R. Felder). July 17(W) to Aug. 22, 6600' to 9000'. **Los Alamos Co.**: VC(CC), GC34(CC). **Rio Arriba Co.**: AS. **Sandoval Co.**: 3 mi. N of PCG, SPD, SJC9, PP, (W).

333c. *Pontia sisymbrii elivata* (Barnes & Benj.). April 13 to June 4, 6500' to 9200'. **Los Alamos Co.**: Los Alamos (CC). **Rio Arriba Co.**: 4 mi. NE of Gallina, 4 mi. N of El Rito. **Sandoval Co.**: SPD, BC4, PP, PC4, (W). **Santa Fe Co.**: GC31(SJC).

334. *Pontia protodice* (Boisd. & Leconte). April 15(W) to Sept. 16, 5500' to 9000'. **Los Alamos Co.**: VC(CC), Los Alamos (CC), BuM(SJC). **Rio Arriba Co.**: J, LS, GMu, MC, EVD. **Sandoval Co.**: 1 mi. up BC from BC4, FC, SBH, SSH, 6 mi. NW of SPD, CCr, road up CPl, 2.5 mi. up road to PP (W, as *Pieris occidentalis* Reakirt and *Pieris occidentalis calyce* W. H. Edwards). **Santa Fe Co.**: Bk(CC).

336h. *Pieris napi mcdunnoughi* Remington. May 10(W) to July 9 and July 31 to Aug. 26, 6200' to 9300'. **Los Alamos Co.**: LAR, VC(CC). **Rio Arriba Co.**: SPP(SJC). **Sandoval Co.**: SPC, CCG, 3 mi. N of PCG, 10 mi. N of PCG, 4 mi. S of B in BC, RCP, 5 mi. E of Regina in SJsC, 1.5 mi. N of RLC on USFS Road 534, SS, (W, as *Pieris napi pallida* Scudder).

338. *Pieris rapae* (L.). June 11 to Sept. 16, 5700' to 7200'. **Los Alamos Co.**: Los Alamos, VC(SJC). **Rio Arriba Co.**: 1 mi. SE of A. **Sandoval Co.**: Jemez Springs, Cuba.

343c. *Euchloe hyantis lotta* Beut. May 12 to June 4, 7000' to 9200'. **Rio Arriba Co.**: EVD, 3 mi. W of Gallina (JAS). **Sandoval Co.**: PP.

348b. *Anthocharis sara inghami* Gunder. April 10(W) to June 11, 5500' to 8500'. **Los Alamos Co.**: VC(CC), GC34(CC). **Rio Arriba Co.**: PCr, 3 mi. W of Gallina (JAS). **Sandoval Co.**: BC4, PC4, FC, 4 mi. E of Regina in SJcC, CCr, LJC, (W, as *Anthocharis sara reakirti* (W. H. Edwards)). **Santa Fe Co.**: SFD.

351c. *Colias philodice eriphyle* W. H. Edwards. May 30 to +July 15, 6200' to 9200'. **Los Alamos Co.**: VC(CC), CMy(SJC). **Rio Arriba Co.**: 1 mi. S of LCt, 6 mi. E of CM, GPk. **Sandoval Co.**: 4 mi. below B in BC, 2 mi. N of SSH, PC4, SCC6.

352. *Colias eurytheme* Boisd. May 6 to Oct. 27, 5500' to 9000'. **Los Alamos Co.**: VC(CC), GC34(CC), WR(CC), BuM(SJC), CMy(SJC). **Rio Arriba Co.**: DLO, 2 mi. S of DM, 1 mi. S of EVD(MT). **Sandoval Co.**: 1 mi. N of BC4, FC, 2 mi. N of SSH, CCr, 2.5 mi. up road to PP, 1 mi. N of PCG in PCn, (W, as *C. e. ariadne* W. H. Edwards, *C. e. keewaydin* W. H. Edwards, and *C. e. pallida* Cockerell).

355a. *Colias alexandra alexandra* W. H. Edwards. June 3 to July 31, 7200' to 9800'. **Los Alamos Co.**: GC34, VC(CC), LASA. **Rio Arriba Co.**: LCt, CPL, TC, GlT, T18, R. **Sandoval Co.**: SPD, DCr, RLC, RT.

368a. *Zerene cesonia cesonia* (Stoll). May 15 to Aug. 6, 5200' to 8300'. **Rio Arriba Co.**: MC, Rio Chama below DM(SJC). **Sandoval Co.**: RGp, SYD, BC(CC), La Jara Creek NE of Cuba (JAS & GS), (W).

380. *Eurema mexicanum* (Boisd.). May 7 and May 13, 5500' to 6000'. **Sandoval Co.**: CCr, FC.

383. *Eurema lisa* (Boisd. & Leconte). **Sandoval Co.**: Jemez Springs (JW(?), det. CDF; specimen in the Carnegie Museum).

388. *Eurema nicippe* (Cramer). May 8 to +July 27, 6000' to 8800'. **Los Alamos Co.**: VC(CC), Los Alamos (CC). **Rio Arriba Co.**: Cerro Blanca N of Gallina (GS). **Sandoval Co.**: 2 mi. N of B, FC, 2 mi. N of SSH, (W).

389. *Nathalis iole* Boisd. May 6(W) to Oct. 13, 6500' to 9800'. **Los Alamos Co.**: VC(CC), Los Alamos (CC), PSA(SJC), BuM(SJC), CMy(SJC). **Rio Arriba Co.**: MC, 1 mi. S of EVD(MT), SPP(SJC), 6 mi. E of Gallina (GS). **Sandoval Co.**: SSH, FC(CC), PCG(CC), (W).

LYCAENIDAE

392d. *Tharsalea arota schellbachi* Tilden. July 3(W) to Aug. 29, 6200' to 9000'. **Los Alamos Co.**: Los Alamos (CC), LAR(SJC). **Rio Arriba Co.**: PrCr, CT. **Sandoval Co.**: 4 mi. down BC from B, PC4, TS, SJC4, PP, (W, as *Chrysophanus arota virginiensis* W. H. Edwards).

401a. *Chalceria heteronea heteronea* (Boisd.). July 31 to Aug. 12, 7600' to 8000'. **Rio Arriba Co.**: AS. **Sandoval Co.**: 1 mi. N of Regina, BPL.

404. *Epidemia helloides* (Boisd.) complex. May 28 to Sept. 11, 6500' to 9800'. **Los Alamos Co.**: CMy(SJC), LASA(SJC). **Rio Arriba Co.**: 3 mi. N of CR, 4 mi. W of DLO, RdO 2 mi. above SL, 1 mi. E of NM Hwy 595 on NM Hwy 96, AS, 77, 1 mi. below ST towards MC, GlT. **Sandoval Co.**: PP4, SPC, 3 mi. N of PCG, CSc, RGp7, BD, PC4, BPL.

408a. *Hypaurotis crysalus crysalus* (W. H. Edwards). July 8 to Sept. 17, 6200' to 9800'. **Los Alamos Co.**: LAR, PSA(SJC). **Rio Arriba Co.**: AS, 1 mi. E of R. **Sandoval Co.**: 4 mi. down BC from B, 3 mi. N of PCG, RGp6, TS, (W).

412b. *Atlides halesus estesi* Clench. July 13–21. **Los Alamos Co.**: WR(CC).

417d. *Harkenclenus titus immaculosus* (Comstock). July 21 to Aug. 6, 7800'. **Sandoval Co.**: PC4, CCG(CDF).

418b. *Satyrium behrii crossi* (Field). May 11 to July 11(W), 6200' to 9000'. **Los Alamos Co.**: BuM(SJC & DH). **Rio Arriba Co.**: LS, MC, near A(SJC), GPk(SJC). **Sandoval Co.**: 2 mi. up road to PP, Jemez Springs, PP, RGp6, (W). **Santa Fe Co.**: GC31.

422. *Satyrium sylvinum itys* (W. H. Edwards). June 9 to Aug. 12, 5600' to 8000'. **Rio Arriba Co.**: AS, 2 mi. down Rio Chama from A. **Sandoval Co.**: Gilman, BPL, (W).

424c. *Satyrium calanus godarti* (Field). June 25(W) to Aug. 26, 6200' to 8900'. **Los Alamos Co.**: LAR, BuM(SJC). **Rio Arriba Co.**: AS, 1 mi. S of EVD(MT). **Sandoval Co.**: 4 mi. down BC from B, SPD, 6 mi. NW of SPD, TS, PC4, RGp6, (W).

430a. *Satyrium saepium saepium* (Boisd.). **Los Alamos Co.**: GC34(CC, probable misdetermination or mislabelling).

433. *Ministrymon leda* (W. H. Edwards). June 21, 6500'. **Rio Arriba Co.**: Rio Chama below DM(SJC).

446a. *Callophrys apama apama* (W. H. Edwards). May 14(W) to Aug. 27, 6500' to 9200'. **Los Alamos Co.**: GC34, BuM(SJC). **Rio Arriba Co.**: RdO at SL, NMJ1, GMu, 77. **Sandoval Co.**: PP, 4 mi. S of Jemez Springs, Rio Guadalupe 1 mi. N of tunnels, 6 mi. NW of SPD, CY, 3 mi. NE of PCG, (W).

452. *Mitoura spinetorum* (Hew.). April 20(W) to July 16, 6500' to 9500'. **Los Alamos Co.**: VC(CC), GC34(CC), Los Alamos (CC), CMy(SJC). **Rio Arriba Co.**: 3 mi. N of CR, 1 mi. down Mine Canyon from ST. **Sandoval Co.**: 2.5 mi. up road to PP, 2 mi. N of Jemez Springs, 3 mi. NE of PCG, LJC, (W).

458a. *Mitoura siva siva* (W. H. Edwards). May 2 to Aug. 20, 5500' to 8000'. **Los Alamos Co.**: WR, Los Alamos (CC). **Rio Arriba Co.**: E4, GMu, MC, MCd, 1 mi. S of EVD(MT). **Sandoval Co.**: CCr, FC, 2.5 mi. up road to PP, SJC9, 6 mi. NW of Cochiti Pueblo, RGp, (W, as *Thecla castalis* W. H. Edwards).

463. *Sandia mcfarlandi* Ehrlich & Clench. June 7, 7000'. **Sandoval Co.**: PrCn. Two *S. mcfarlandi* were taken by RH in 1980 during a Mountain Club outing. The foodplant, *Nolina texana*, is not found many places in the Jemez. Repeated whacking of the foodplant around Jemez Springs in 1983–1985 failed to flush any additional adults.

464d. *Incisalia augustinus iroides* (Boisd.). May 12–14(W), also May 20, 8000'. **Sandoval Co.**: 1 mi. N of FL(SJC), (W, as *augustus* (Kirby)).

465. *Incisalia fotis* (Strecker). April 22, 1916. **Sandoval Co.**: Jemez Springs (JW, specimen in Allyn Museum of Entomology). This species was recorded by Woodgate but has never been taken again in the Jemez.

466b. *Incisalia polia obscura* Ferris & Fisher. April 16 to June 19, 8000' to 10,000'. **Los Alamos Co.**: road to CMy at 8000'(SJC & DH). **Rio Arriba Co.**: LMP, 1 mi. N of CR. **Sandoval Co.**: FL(RAB), FL(SJC), CCG(CDF), Jemez Springs (JW, specimen in Carnegie Museum, but not on Williams' 1914 list).

471a. *Incisalia eryphon eryphon* (Boisd.). April 13 to July 3, 6500' to 8500'. **Los Alamos Co.**: GC34, VC(CC), CMy(SJC). **Rio Arriba Co.**: LCt, RCG, RdO 1 mi. above SL. **Sandoval Co.**: RGp6, 4 mi. E of Regina in SJsC, PP4, (W).

478c. *Strymon melinus franki* Field. April 23 to Sept. 17, 5500' to 9000'. **Los Alamos Co.**: GC34, RC(CC), BuM(SJC), VC(SJC). **Rio Arriba Co.**: E4, LS, 1 mi. S of EVD(MT). **Sandoval Co.**: 4.5 mi. NW of Cochiti Pueblo, TR, RGp6, CY, NM Hwy 44 at road to PP, (W).

495. *Brephidium exile* (Boisd.). June 16 to Nov. 9, 5200' to 6500'. **Los Alamos Co.**: Los Alamos (CC). **Rio Arriba Co.**: 1 mi. S of EVD(MT). **Sandoval Co.**: HGP, Jemez Springs, SYD.

497b. *Leptotes cassius striata* (W. H. Edwards). Aug. 1, 6800'. **Rio Arriba Co.**: 1 mi. S of EVD (MT, very surprising record, possibly *marina* (Reakirt) aberration). RH has seen the specimen, and is uncertain as to its affinity; the data are certain.

498. *Leptotes marina* (Reakirt). April 20(W) to Oct. 7, 5600' to 8600'. **Los Alamos Co.**: GC34(CC), BuM(SJC), VC(SJC). **Rio Arriba Co.**: PrCr, LCt, Jct. of US Hwy 285 and NM Hwy 96 (JAS). **Sandoval Co.**: LoS, 3 mi. N of PCG, RLC, HC, SPD, Gilman, (W). **Santa Fe Co.**: SFC, CG31.

502a. *Hemiargus isola alce* (W. H. Edwards). April 7 to Oct. 14(W), 6000' to 9800'. **Los Alamos Co.**: Los Alamos (CC), GC34(CC), BuM(SJC), VC(SJC), CMy(SJC). **Rio Arriba Co.**: LCt, 77, 1 mi. S of EVD(MT). **Sandoval Co.**: PP, 2 mi. N of SSH, 4 mi. E of Regina in SJsC, FC(SJC), (W).

504. *Everes amyntula* (Boisd.). April 7 to Aug. 26, 6000' to 9800'. **Los Alamos Co.**: Los Alamos (CC), BuM(SJC), PSA(SJC), CMy(SJC). **Rio Arriba Co.**: MC, 1 mi. S of EVD(MT). **Sandoval Co.**: 1 mi. N of BC4 in BC, SBH, CY, BC4, road up CPl, SMC, PP4, (W). **Santa Fe Co.**: GC31.

505h. *Celastrina argiolus cinerea* (W. H. Edwards). May 6 to Sept. 6, 6500' to 9600'. **Los Alamos Co.**: BuM(SJC). **Rio Arriba Co.**: CT, EM(JAS & GS). **Sandoval Co.**: B, BC4, PP4, 4 mi. E of Regina in SJsC, PC4, (W, as *Lycaena ladon cinerea* W. H. Edwards and *Lycaena ladon arizonensis* W. H. Edwards).

508a. *Euphilotes battoides centralis* (Barnes & McD.). July 11 to Aug. 18, 6000' to 8400'. **Rio Arriba Co.**: 1 mi. S of EVD(MT). **Sandoval Co.**: 1.5 mi. below crest near TS,

3.5 mi. up road to PP, 20 mi. S of Cuba on NM Hwy 44, FC(OS & SLE), Jemez Springs (JW(?), Carnegie Museum coll.). **Santa Fe Co.**: GC31.

509a. *Euphilotes enoptes ancilla* (Barnes & McD.). No date, 8000'. **Sandoval Co.**: Jemez Springs (AMNH, probable misdetermination).

511a. *Euphilotes rita rita* (Barnes & McD.). July 30 to Sept. 17, 5500' to 6700'. **Sandoval Co.**: 4.5 mi. NW of Cochiti Pueblo, TR, HGS, NM Hwy 197 8 mi. S of junction with NM Hwy 44 (OS & SLE), FC(SJC).

511c. *Euphilotes spaldingi* (Barnes & McD.). July 12 to Aug. 3, 8000'. **Rio Arriba Co.**: AS, LCt (hundreds), 1 mi. S of EVD(MT). The swarming of this usually rare butterfly at LCt has no precedent in our experience.

513d. *Glaucopsyche piasus daunia* (W. H. Edwards). No date or elevation. **Sandoval Co.**: Jemez Pueblo (Carnegie Museum coll.; this may be a Woodgate specimen; if so, it would be a second species recorded by Woodgate, but not observed since then.).

514f. *Glaucopsyche lygdamus oro* (Scudder). May 7 to June 24, 6000' to 10,000'. **Los Alamos Co.**: Los Alamos (CC), CMy(SJC), BuM(SJC). **Rio Arriba Co.**: 1 mi. N of CR, CT, CyCn, Rio Chama below DM(SJC). **Sandoval Co.**: 1 mi. up BC from BC4, SPC, 4 mi. E of Regina in SJsC, USFS Road 534 1.5 mi. N of RLC, 2 mi. N of NM Hwy 44 on NM Hwy 96 (W, as *Lycaena behri* W. H. Edwards; see Brown 1970 for explanation).

517b. *Lycaeides melissa melissa* (W. H. Edwards). May 13(W) to Aug. 29, 5600' to 8700'. **Los Alamos Co.**: GC34(CC), VC(CC), BuM(SJC), CMy(SJC). **Rio Arriba Co.**: AD, 77, 2 mi. N of Gallina, 1 mi. down Mine Canyon from ST, AS, 1 mi. S of EVD(MT), Rio Chama below DM(SJC). **Sandoval Co.**: 2 mi. up road to PP, 2 mi. N of Jemez Springs, PP, RGp, FC(CC), BC(CC), NM Hwy 197 8 mi. SW of junction with NM Hwy 44 (OS & SLE), (W).

518b. *Plebejus saepiolus whitmeri* F. M. Brown. June 14 to July 26, 7800' to 11,000'. **Los Alamos Co.**: PSA, VC(CC), Los Alamos (CC), CMy(SJC). **Rio Arriba Co.**: CSc, CM. **Sandoval Co.**: BD, E side of VG, 2 mi. N of SSH, LCC, 17 mi. W of BNMJ on NM Hwy 4, BGB, PC4.

520b. *Icaricia icarioides lycea* (W. H. Edwards). May 27 to July 28, 7000' to 9800'. **Los Alamos Co.**: LASA(SJC), BuM(SJC), CMy(SJC). **Rio Arriba Co.**: 4 mi. W of Regina in SJsC, 13 mi. W of Española on USFS Road 144, AS, 2 mi. E of PC, CT, DC, GPk, ST, GT. **Sandoval Co.**: PP4, Señorito Canyon (JAS & GS), (W, as *Lycaena fulla* W. H. Edwards).

522b. *Icaricia acmon texana* Goodpasture. April 12 to Sept. 17, 5500' to 8000'. **Los Alamos Co.**: VC(CC), GC34(CC), BuM(SJC), CMy(SJC). **Rio Arriba Co.**: LCt, 1 mi. S of EVD(MT), Rio Chama below DM(SJC). **Sandoval Co.**: FC, TR, 4.5 mi. NW of Cochiti Pueblo, HGS, Jemez Springs, PP4, (W). **Santa Fe Co.**: SFD.

526e. *Agriades rusticus rusticus* (W. H. Edwards). May 28 to July 26, 7400' to 11,500'. **Los Alamos Co.**: GC34, LASA, VC(CC), CMy(SJC). **Rio Arriba Co.**: CM, RdO 2 mi. W of SL, 1.5 mi. N of DC, CSt, T18. **Sandoval Co.**: SBH, RLC, 2 mi. N of SSH, 1.5 mi. S of NM Hwy 4 near SPD, PP, 4 mi. E of Regina in SJsC, PC4, (W, as *Lycaena podarce* C. & R. Felder).

RIODINIDAE

544e. *Apodemia mormo mormo* (C. & R. Felder). Aug. 6 to Sept. 9, 6000' to 7500'. **Rio Arriba Co.**: 1 mi. E of NMJ1, Rio Chama below DM(SJC). **Sandoval Co.**: HGS, BPL, Regina, 8 mi. NW of San Ysidro (OS & SLE, as *cythera* (W. H. Edwards)).

550. *Apodemia nais* (W. H. Edwards). June 17 to Aug. 25, 6200' to 9000'. **Los Alamos Co.**: VC(CC), GC34(CC), BuM(SJC). **Rio Arriba Co.**: GMu, vic. GPk(SJC). **Sandoval Co.**: BC 4 mi. below B, 6 mi. NW of SPD, TS, BC4, PP, (W).

LIBYTHEIDAE

552a. *Libytheana bachmanii larvata* (Strecker). Aug. 26, 5400'. **Sandoval Co.**: 3.5 mi. NW of Cochiti Pueblo.

NYMPHALIDAE

562. *Euptoieta claudia* (Cramer). April 29 to Sept. 19, 6500' to 9800'. **Los Alamos Co.**: LAR(SJC), PSA(SJC), BuM(SJC), VC(SJC). **Rio Arriba Co.**: MC, 1 mi. S of EVD(MT), SPP(SJC), EM(SJC). **Sandoval Co.**: 6 mi. W of San Ysidro on NM Hwy 44 (MT), FC(SJC), Señorito 5 mi. SE of Cuba (SJC), LJC(SJC), (W).

565e. *Speyeria cybele carpenterii* (W. H. Edwards). July 9 to Aug. 26, 6500' to 8900'. **Los Alamos Co.**: LAR. **Sandoval Co.**: 3 mi. N of PCG, 4 mi. down BC from B, SPD, 1 mi. above SJC4, Jemez Springs (W. H. Howe), LCC(W. H. Howe).

568g. *Speyeria aphrodite ethne* (Heming). July 31, 8500'. **Los Alamos Co.**: LAR(SJC). This and the next record are surprising but almost certainly valid.

569. *Speyeria edwardsii* (Reakirt). June 13 to June 17, 8200'. **Rio Arriba Co.**: BrCn (leg. L. H. Martinez; ex. UNM coll.; data certified by C. Crawford, Univ. New Mexico Biology Dept.), vic. GPk(SJC).

574e. *Speyeria atlantis nikias* (Ehrmann). June 9 to Sept. 20(W), 6200' to 10,500'. **Los Alamos Co.**: 1 mi. W of GC34, LAR(SJC), PSA(SJC), VC(SJC). **Rio Arriba Co.**: 1 mi. S of EPL, 1 mi. N of CM, 1 mi. S of LCt, AS, CSt, 1.5 mi. N of DC, EM. **Sandoval Co.**: 4 mi. down BC from B, SPD, 10 mi. N of PCG, 1 mi. N of RoC, TS, .5 mi. N of NM Hwy 126 on USFS Road 144, 1 mi. above SJC4, (W, as *Argynnis bremnerii* W. H. Edwards, the type series of *Argynnis nikias* Ehrmann).

576i. *Speyeria mormonia eurynome* (W. H. Edwards). July 7 to +Aug. 1, 8000' to 10,100'. **Los Alamos Co.**: PSA. **Rio Arriba Co.**: 1 mi. S of EPL, CR, VLG, R. **Sandoval Co.**: E side of VG, 1.5 mi. SW of NM Hwy 4 on road to SPD, 2 mi. N of SSH, TCC, 1 mi. N of RoC, CCG, BrC.

579d. *Clossiana selene tollandensis* (Barnes & Benj.). July 4 to July 18, 8200' to 8500'. **Sandoval Co.**: BD, TCC, Cebolla Creek (AMNH coll.).

589f. *Clossiana titania helena* (W. H. Edwards). July 15 to Aug. 31, 8500' to 10,500'. **Los Alamos Co.**: PSR, PSA(SJC). **Rio Arriba Co.**: 1 mi. N of CM, CR, CSc, NRP. **Sandoval Co.**: TCC, RoC, 3–5 mi. NE of SS(SJC).

592. *Poladryas minuta arachne* (W. H. Edwards). May 20 to Sept. 8, 7000' to 9000'. **Rio Arriba Co.**: DLO, DC, 1 mi. S of EVD(MT), Rio Chama below DM(SJC). **Sandoval Co.**: PC4, 10 mi. N of Jemez Springs (AMNH coll.), FL(SJC), (W).

596. *Thessalia fulvia* (W. H. Edwards). May 25 to Sept. 16, 5300' to 8000'. **Rio Arriba Co.**: 2 mi. E of PC, AD, LS, NMJ1, 77, DM, GlT, 1 mi. S of EVD(MT). **Sandoval Co.**: 5 mi. S of SPD, PP4, BPL, HGS, NM Hwy 44 at road to PP, NMJ2, 8 mi. S of Cuba on NM Hwy 197, (W). **Santa Fe Co.**: TP, Bk.

598. *Chlosyne lacinia crocale* (W. H. Edwards). June 13 to +July 15, 7800' to 8500'. **Sandoval Co.**: CCr, 1 mi. W of Santo Domingo Pueblo.

605b. *Charidryas gorgone carlota* (Reakirt). May 14(W) to June 27, 8000' to 9100'. **Los Alamos Co.**: GCR(Colorado Univ. coll.). **Rio Arriba Co.**: RtC, AS, PCr. **Sandoval Co.**: RT, SBH, SPC, (W, as *Phyciodes ismeria* (Boisd. & Leconte)).

606b. *Charidryas nycteis drusius* (W. H. Edwards). June 13 to July 15, 7800' to 8500'. **Los Alamos Co.**: GCR, VC(SJC). **Sandoval Co.**: CCG, BD, RLC, 4 mi. N of PCG, SPC, TCC, SJoC.

609. *Charidryas acastus acastus* (W. H. Edwards). May 19 to June 18, 5400' to 9500'. **Rio Arriba Co.**: SPP(SJC), Gallina(GS). **Sandoval Co.**: NMJ2, SYD, Mahan Canyon 3 mi. E of Regina (GS), near Cuba (RAB), (W).

623b. *Phyciodes tharos* (Drury), Type A. Sept. 3 to Sept. 19, 5000' to 6000'. **Sandoval Co.**: 1 mi. W of Santo Domingo Pueblo, 3 mi. N of San Felipe Pueblo, FC(SJC).

623d. *Phyciodes tharos* (Drury), Type B. May 20(W) to Aug. 5, 6500' to 8500'. **Los Alamos Co.**: LASA, LAR(SJC), VC(SJC). **Rio Arriba Co.**: AS, MC, DC, LJT, T18, 4 mi. N of Gallina (SJC), vic. GPk(SJC), Rio Chama below DM(SJC). **Sandoval Co.**: HM, PC4, SPC, 10 mi. N of Jemez Springs (AMNH coll.), 1 mi. S of SSH(SJC), Mahan Canyon (SJC), (W, presumed Type B).

625c. *Phyciodes pratensis camillus* W. H. Edwards. May 8 to Sept. 9, 5400' to 9800'. **Los Alamos Co.**: LAR(SJC), BuM(SJC), CMy(SJC), VC(SJC). **Rio Arriba Co.**: VLG, PrCr, CyCn, 4 mi. W of DLO, WHT, 1 mi. S of EVD (MT). **Sandoval Co.**: BC4,

RT, HGS, SCC6, 4 mi. E of Regina in SJsC, BR, BPL, SYD, 77, 17 mi. W of BNMJ on NM Hwy 4 (MT), (W).

626a. *Phyciodes pictus pictus* W. H. Edwards. May 19 to Aug. 28, 5400' to 6500'. **Rio Arriba Co.**: AD, junction of US Hwy 84 and US Hwy 285 near Española, 1 mi. N of Youngsville (JAS & GS). **Sandoval Co.**: HGS, 4 mi. S of Jemez Springs, SYD, (W).

629b. *Phyciodes mylitta arizonensis* Bauer. May 2 to Aug. 31, 6000' to 9000'. **Los Alamos Co.**: GC34, BuM(SJC). **Rio Arriba Co.**: Br, Rio Gallina at edge of SPP(JAS & GS). **Sandoval Co.**: 1 mi. up BC from BC4, FC, PC4, SPC, 5 mi. E of Regina in SJsC, LJC, (W).

631a. *Occidryas anicia alena* (Barnes & Benj.). May 5 to June 17, 6500' to c. 8000'. **Rio Arriba Co.**: Gallina (JAS & GS), vic. GPk(SJC), Cerro Blanca N of Gallina (JAS & GS), Rio Chama below DM(SJC). **Sandoval Co.**: AMNH has a specimen from the Jemez dated 5 May 1913. There is no mention of this specimen (or this species) in Williams (1914), although it is hard to imagine another collecter in the Jemez on this date. The record is definitely plausible and indicates that Woodgate did not dispose of his Jemez material from 1912–1913 exclusively to Williams.

638a. *Polygonia satyrus satyrus* (W. H. Edwards). May 6 to May 23 and July 3 to +July 17, 6000' to 9800'. **Los Alamos Co.**: PSA(SJC), VC(SJC). **Sandoval Co.**: 2 mi. N of B, FC, HM, 1 mi. N of PCG in PCn. **Rio Arriba Co.**: PrCr, LJT.

639e. *Polygonia faunus hylas* (W. H. Edwards). April 7 to June 19 and Aug. 5 to Nov. 10(W), 6500' to 9500'. **Los Alamos Co.**: LAR, CMy(SJC). **Rio Arriba Co.**: CSc, 4 mi. E of Regina in SJsC, SPP(SJC). **Sandoval Co.**: BGB, RCP, 1 mi. N of RLC on USFS Road 534, SS, BPL, 1 mi. N of PCG in PCn, (W). **Santa Fe Co.**: GC31.

642. *Polygonia zephyrus* (W. H. Edwards). April 7 to July 31(W) and Sept. 8 to Oct. 6, 7000' to 10,000'. **Los Alamos Co.**: PSA, LAR(SJC), VC(SJC). **Rio Arriba Co.**: VLG, J, 4 mi. W of DLO, CT, WHT, MG. **Sandoval Co.**: 2 mi. N of B, HM, SS, 4 mi. above CCr on road to SPD, (W, as *Grapta silvius* W. H. Edwards). **Santa Fe Co.**: Caja del Rio Plateau (SJC).

647a. *Nymphalis californica californica* (Boisd.). May 2 to July 7, 6500' to 10,100'. **Los Alamos Co.**: PSA. **Rio Arriba Co.**: CdG, 4 mi. NE of Gallina (SJC), GPk(SJC) **Sandoval Co.**: SPD, BC4, HM, LJC.

648a. *Nymphalis antiopa antiopa* (L.). April 12 to Sept. 17(W), 6000' to 9800'. **Los Alamos Co**: LAR(SJC), PSA(SJC), CMy(SJC), VC(SJC). **Rio Arriba Co.**: SPP(SJC), near A(SJC), 4 mi. NE of Gallina (SJC). **Sandoval Co.**: SSH, FC(SJC), (W).

649b. *Aglais milberti milberti* (Godart). May 6 to July 31, 7800' to 9800'. **Los Alamos Co**: BuM(SJC), LAR(SJC), PSA(SJC). **Sandoval Co.**: 2 mi. N of B, PC4, 17 mi. W of BNMJ, (W).

650. *Vanessa virginiensis* (Drury). May 7 to +July 31, 6800' to 9800'. **Los Alamos Co.**: LAR(SJC). **Rio Arriba Co.**: GT, 1 mi. S of EVD(MT). **Sandoval Co.**: SPD, PP, SBH, LCC(RL).

651. *Vanessa cardui* (L.). April 11 to Sept. 19, 6000' to 9800'. **Los Alamos Co.**: PSA(SJC), LAR(SJC), BuM(SJC), CMy(SJC). **Rio Arriba Co.**: MC, 3 mi. W of Gallina (JAS), 1 mi. S of EVD(MT). **Sandoval Co.**: SBH, 1 mi. W of Regina (JAS), (W). **Santa Fe Co.**: Tsan Kawi Ruins, Bandelier National Monument (northern section) (RL).

652. *Vanessa annabella* (Field). May 7 to Aug. 31, 6000' to 9800'. **Los Alamos Co.**: PSA(SJC). **Sandoval Co.**: SPD, FC, SBH, BrC, LCC(RL). **Rio Arriba Co.**: Br, Rio Chama below DM(SJC).

653a. *Vanessa atalanta rubria* (Fruhst.). May 13 to Oct. 6, 6000' to 9800'. **Los Alamos Co.**: PSA(SJC). **Rio Arriba Co.**: SPP(SJC). **Sandoval Co.**: FC, SBH, 2 mi. N of SSH, above CCr, (W).

656. *Junonia coenia* Hubner. May 28 to Sept. 17, 5000' to 8400'. **Rio Arriba Co.**: RdO at SL. **Sandoval Co.**: TR, Jemez Springs, SPC, BPL, 3 mi. N of San Felipe Pueblo, SJoC, SJC4. **Santa Fe Co.**: GMu near SFD.

664a. *Limenitis archippus archippus* (Cramer). Aug. 5 to Sept. 19, 5800' to 6000'. **Rio Arriba Co.**: 2 mi. down Rio Chama from A, Rio Chama below DM(SJC). **Sandoval Co.**: P at San Juan Mesa Rd. (This is the only known *L. archippus* record from the

Rio Puerco drainage.) **Santa Fe Co.**: GMu near SFD, Sunrise Spring near SFD, NM Hwy 4 near NM Hwy 30 near Rio Grande (SJC).

665b. *Limenitis weidemeyerii weidemeyerii* (W. H. Edwards). June 2 to Aug. 29, 6500' to 10,000'. **Los Alamos Co.**: PSA, LAR(SJC), VC(SJC). **Rio Arriba Co.**: MCd, MCr, 1 mi. S of EVD(MT). **Sandoval Co.**: RGp6, RLC, PC4, SPC, PR, HC, (W). **Santa Fe Co.**: GC31.

668a. *Adelpha bredowii eulalia* (Doubleday & Hew.). June 11 to Sept. 19, 6000' to 8900'. **Los Alamos Co.**: Water Canyon (SJC), VC(SJC). **Rio Arriba Co.**: 1 mi. N of Gallina (SJC), GPk(SJC), Rio Chama below DM(SJC). **Sandoval Co.**: 14 mi. NW of Cochiti Pueblo near BS, LoS, 1–4 mi. N of PCG, BC, FC(SJC).

695. *Anaea andria* Scudder. Sept. 3, 5100'. **Sandoval Co.**: 1 mi. W of Santo Domingo Pueblo, 1 mi. S of Cochiti Dam (JAS).

717a. *Cyllopsis pertepida dorothea* (Nabokov). June 3 to Sept. 19, 5500' to 8000'. **Los Alamos Co.**: RoC. **Rio Arriba Co.**: 2 mi. S of A, 1 mi. S of LCt, PrCr, 1 mi. S of EVD(MT). **Sandoval Co.**: TR, PC4, TS, FC(SJC), (W, as *Neonympha henshawi* (W. H. Edwards)).

729b. *Coenonympha ochracea ochracea* W. H. Edwards. May 28(W) to July 3, 6600' to 10,000'. **Los Alamos Co.**: BuM(SJC). **Rio Arriba Co.**: PrCr, CP, 13 mi. W of Española on USFS Road 144, LCt, 1.5 mi. N of DC, LJT, 1 mi. E of LJT, MCr, 1 mi. S of EVD(MT). **Sandoval Co.**: PP, RLC, SSH, 4 mi. N of PCG, (W).

732h. *Cercyonis pegala boopis* (Behr). July 1 to Aug. 29, 5300' to 8400'. **Rio Arriba Co.**: 2 mi. S of A, CC, 1 mi. SE of A, 5 mi. S of DM, MC, 1 mi. S of EVD(MT). **Sandoval Co.**: SPD, SJC9, 1.5 mi. up road to PP, FC(OS & SLE), (W, as *Satyrus alope ariane* (Boisd.)). **Santa Fe Co.**: GMu near SFD, Bk, GC31.

733a. *Cercyonis meadii meadii* (W. H. Edwards). Aug. 9 and Aug. 22(W), 7000'. **Sandoval Co.**: (W, 1 female). **Santa Fe Co.**: Sunrise Spring near SFD (sight, large female). This species has an erratic distribution and abundance, and its phenotype varies from range to range. We believe the reports from the Gila Mountains are also valid.

735a. *Cercyonis oetus charon* (W. H. Edwards). May 9 to Sept. 16, 7500' to 10,000'. **Los Alamos Co.**: LASA, LAR(SJC). **Rio Arriba Co.**: CSc, LCt, CP, AS, TC, GlT, 1 mi. S of EVD(MT). **Sandoval Co.**: HM, LS, PP, SPD, 3 mi. N of PCG, USFS Road 144 .5 mi. N of NM Hwy 126, SJoC, 77, (W, as *Satyrus silvestris* W. H. Edwards).

748a. *Neominois ridingsii ridingsii* (W. H. Edwards). June 30, 9000'. **Rio Arriba Co.**: LoM, LS, Rio Gallina at SPP(JAS).

752d. *Oeneis chryxus chryxus* (Doubleday & Hew.). May 28 to July 15, 7600' to 10,000'. **Los Alamos Co.**: PSA, CMy(SJC). **Rio Arriba Co.**: RtC. **Sandoval Co.**: BD, RLC, UNM, RoC, CPl, (W).

760. *Danaus plexippus* (L.). May 8 to Aug. 28 and Nov.(W), 6000' to 9800'. **Los Alamos Co.**: PSA(SJC). **Rio Arriba Co.**: Rio Chama below DM(SJC), Española (SJC), near A(SJC). **Sandoval Co.**: 2 mi. N of B, FC, HGP, (W).

761b. *Danaus gilippus strigosus* (Bates). June 24 to +July 31, 6500'. **Rio Arriba Co.**: DM, 1 mi. S of EVD(MT), Rio Chama below DM(SJC). **Sandoval Co.**: 3 mi. S of Cuba, SJsC(SJC), (W).

DISCUSSION

The Jemez Mountains of north-central New Mexico are now known to support 155 species of butterflies, including components from the Colorado Rockies, the Great Basin, the middle Rio Grande (Upper and Lower Sonoran zones) and even the Great Plains. This compares with 96 species reported from the Jemez by Williams in 1914. All species on the 1914 list were confirmed as extant in the Jemez as of 1985. It is likely that much of the Rocky Mountain element of the Jemez fauna is relictual rather than the result of post-Plesitocene invasion. With the

possible exception of *Speyeria atlantis nikias*, no taxon is endemic to the Jemez, and even *S. a. nikias* blends gradually with *S. a. hesperis* (W. H. Edwards) in the ranges to the north of the Jemez. The total of 155 species gives the Jemez the second most diverse fauna of the New Mexican mountain ranges, exceeded only by the Gila Mountains (165 species). Lower Sonoran and Arctic-Alpine zones do not occur in the Jemez, thus making the species diversity there all the more impressive.

Fifteen species—*Erynnis meridianus, Satyrium saepium saepium, Leptotes cassius striata, Euphilotes enoptes ancilla, Pyrgus scriptura, Atlides halesus estesi, Sandia mcfarlandi, Incisalia fotis, Glaucopsyche piasus daunia, Speyeria aphrodite ethne, Heliopetes ericetorum, Atalopedes campestris, Eurema lisa, Ministrymon leda,* and *Libytheana bachmanii larvata*—are represented here by a single report. It is conceivable that the first 4 of these records involve misdeterminations. While we have not performed any statistical analyses, having at least 11 species reported only once suggests that a comparable number of species may have been overlooked. Oddly, more resident species (the middle 6 listed above) than migrants or strays (the last 5 listed above) are reported only once. We speculate that more strays have been overlooked in our survey than rare or local resident species.

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MATING FREQUENCY IN BUSH-BROWN BUTTERFLIES (NYMPHALIDAE: SATYRINAE)

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ABSTRACT. Samples of adult female *Mycalesis perseus* (Fabr.), *M. terminus* (Fabr.) and *M. sirius* (Fabr.) (Nymphalidae: Satyrinae) collected over a two-year period during 1989–1990 at Cardwell, north-eastern Australia, were dissected to evaluate their mating frequency based on spermatophore counts. The three species were polyandrous with some individuals mating up to four times. Mating frequency varied seasonally, particularly in *M. perseus,* and in all species the mean number of spermatophores correlated significantly with age-class (extent of wing-wear): 'older' females were more likely to contain more spermatophores than 'younger' females. Despite age effects, significant differences between species were still detected in spermatophore counts, but only among older females. These findings indicate that the variables of relative age and season need to be taken into account when analyzing and comparing mating systems between species of Lepidoptera, particularly tropical butterflies.

Additional key words: insemination, mating behavior, spermatophore number.

Spermatophore counts in Lepidoptera are used widely to determine the number of times a female has mated and infer aspects of the mating system employed (e.g., Burns 1968, Pliske 1973, Wiklund 1977, Ehrlich & Ehrlich 1978, Drummond 1984, Wiklund & Forsberg 1991). Accordingly, female mating systems have been broadly characterized as either monandrous, where all females mate only once during their lifetime, or polyandrous, where most females mate several times during their lifetime. This classification has provided a useful framework in evolutionary studies investigating sexual selection and the adaptive significance of multiple insemination (Svärd & Wiklund 1989, Wiklund & Forsberg 1991, Wiklund et al. 1993 and references therein). In particular, polyandrous species are of considerable interest because it has been shown that male-derived nutrients from spermatophores at mating may be incorporated into both eggs and soma of the mated female (Boggs & Gilbert 1979, Boggs 1981, Boggs & Watt 1981), and females of some species appear to benefit from these nutrients (Rutowski et al. 1987, Watanabe 1988, Oberhauser 1989, Wiklund et al. 1993, but see Boggs 1990 for review).

Satyrine butterflies (Nymphalidae) generally are regarded as being essentially monandrous, or sometimes weakly polyandrous, as multiple insemination is comparatively rare (Ehrlich & Ehrlich 1978, Braby & New 1989, Wiklund & Forsberg 1991). However, Lederhouse et al. (1989) documented some of the pitfalls of using spermatophore data in

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analyzing mating systems. They identified three variables—spermatophore size, wing condition, and date of capture—which may greatly influence the number of times a female mates and therefore distort interpretation of the overall mating system. Moreover, Braby (1995a) recently demonstrated that mean spermatophore number can vary seasonally in tropical satyrines, particularly in species like *Mycalesis perseus* (Fabr.) which breed seasonally—spermatophore counts tend to be higher during the breeding season (wet season) and lower when adults are in reproductive diapause (dry season). These factors need to be considered first before drawing conclusions about female mating systems in general, and before attempting to evaluate the potential role of spermatophores as a nutritional resource in addition to providing sperm.

The aim of this work is to investigate and summarize aspects of mating frequency and behavior in three species of *Mycalesis* Hübner, the 'Bush-browns,' from the Australian tropics. In particular, the effect of wing-wear as an approximate estimate of female age on mating frequency is examined.

MATERIALS AND METHODS

Samples of adult female *Mycalesis perseus, M. terminus* (Fabr.) and *M. sirius* (Fabr.) were collected from a variety of lowland habitats at Cardwell (18°16'S, 146°02'E), north-eastern Queensland, over a two year period during 1989–1990, primarily to study aspects of their reproductive strategies and breeding phenology. The butterflies were killed immediately after capture and transported to the laboratory at Townsville for dissection of the abdomen and examination of the reproductive tract. The sampling procedure, number and frequency of specimens, and laboratory analysis are described by Braby (1995).

The mating state and degree of wing-wear were recorded for each female of each species. The number of spermatophores was counted after dissection of the bursa copulatrix to determine the number of times a female had mated. The extent of wing-wear, as a measure of relative age, was classified subjectively in one of three categories according to the degree of wing tattering and scale loss: fresh = margins entire with none or very few scales missing; slightly worn = margins of one or two wings slightly chipped, 0–5% scales missing; worn = margins of two or more wings chipped, >5% scales missing.

RESULTS

Estimates of female mating frequency, based on spermatophore counts, for the three *Mycalesis* species at Cardwell are presented in Table 1. Pooling these samples over the two year period allows broad comparisons between the species. Two generalisations can be made

TABLE 1. Mating frequency based on spermatophore counts for three species of *Mycalesis*. Percentages given in parentheses. Mating frequency is the total mean number of spermatophores per female.

Species	No. females with spermatophore count of: 0	1	2	3	4	Total examined	Mating frequency
M. perseus	37 (10.9)	220 (64.7)	70 (20.6)	9 (2.7)	4 (1.1)	340	1.18
M. terminus	17 (5.8)	202 (68.7)	71 (24.1)	4 (1.4)	0 (0.0)	294	1.21
M. sirius	18 (5.3)	195 (57.2)	109 (31.9)	18 (5.3)	1 (0.3)	341	1.38

from these data. First, although more than half of the total number of females examined for each species contained one spermatophore, the three *Mycalesis* species were not strictly monandrous and a high frequency of multiple insemination (polyandry) was evident for each. The frequency of polyandry varied from 24.4% in *M. perseus*, (n=83 individuals mated more than once), 25.5% in *M. terminus* (n=75), to 37.5% in *M. sirius* (n=128). Second, differences in overall mating frequency (i.e., the mean number of spermatophores per female) between the species were highly significant (x^2=33.98, df=88, p<0.001). This was mainly attributable to a higher incidence of multiple (second and third) matings in *M. sirius*, a relatively higher proportion of virgins and a lower incidence of multiple (second) matings in *M. perseus*, and a relatively low incidence of multiple (third) matings in *M. terminus*. Both *M. perseus* and *M. terminus* were more similar in mating frequency, although the differences were weakly significant (x^2=10.82, df=4, p=0.029).

How meaningful are these comparative differences in *Mycalesis*? When the frequency distributions of the number of spermatophores were examined in relation to age-class (wing-wear category) an age effect was evident (Table 2). For each species, spermatophore counts were significantly different between the wing-wear categories (*M. perseus*: x^2=91.13, df=8, p<0.001; *M. terminus*: x^2=53.41, df=6, p<0.001; *M. sirius*: x^2=51.63, df=8, p<0.001). That is, mating frequency was correlated with age-class, being lowest in 'younger' females (fresh category) and highest in the 'older' age-class (worn category). More importantly, the differences in spermatophore counts between species detected in Table 1 (age not controlled) did not persist among the 'younger' age-classes when age was controlled (fresh category: x^2=9.25, df=4, p=0.055; slightly worn category: x^2=7.53, df=6, p=0.275) (Table 2). However, among the 'older' age-classes, spermatophore counts between the species were significantly different (worn category: x^2=19.48, df=8, p=0.013). The differences in the older age-class were largely attributable to a higher incidence of multiple matings (three spermatophores) in *M. sirius* and an associated lower frequency of third matings in *M.*

TABLE 2. The number of females (n) with 0, 1, 2, 3 or 4 spermatophores and the mean number of spermatophores for each wing-wear category for three species of *Mycalesis*.

Wing-wear category	Number of spermatophores	*M. perseus*		*M. terminus*		*M. sirius*	
		n	(%)	n	(%)	n	(%)
Fresh	0	29	(33.3)	13	(24.1)	12	(19.4)
	1	52	(59.8)	37	(68.5)	38	(61.2)
	2	6	(6.9)	4	(7.4)	12	(19.4)
	3	0	(0.0)	0	(0.0)	0	(0.0)
	4	0	(0.0)	0	(0.0)	0	(0.0)
	total	87		54		62	
	mean	0.75		0.83		1.00	
Slightly worn	0	7	(9.0)	4	(5.8)	5	(5.8)
	1	61	(78.2)	50	(72.5)	58	(66.3)
	2	10	(12.8)	15	(21.7)	24	(26.7)
	3	0	(0.0)	0	(0.0)	1	(1.2)
	4	0	(0.0)	0	(0.0)	0	(0.0)
	total	78		69		88	
	mean	1.04		1.16		1.21	
Worn	0	1	(0.6)	0	(0.0)	1	(0.5)
	1	107	(61.1)	115	(67.3)	100	(51.8)
	2	55	(31.4)	52	(30.4)	74	(38.4)
	3	8	(4.6)	4	(2.3)	17	(8.8)
	4	4	(2.3)	0	(0.0)	1	(0.5)
	total	175		171		193	
	mean	1.47		1.35		1.57	

terminus and single matings in *M. sirius*; curiously, there was also a relatively high incidence of fourth matings in *M. perseus*. Hence, despite age affects, differences in mating frequency between the three species were real but only significant among 'older' females with *M. sirius* (47.7% of worn females mated more than once; mean number of spermatophores per female 1.57) and *M. perseus* (38.3% of worn females mated more than once; mean number of spermatophores per female 1.47) having a higher frequency of polyandry than *M. terminus* (32.7% of worn females mated more than once; mean number of spermatophores per female 1.35).

Observations on the daily and seasonal incidence of matings for *M. perseus* and *M. terminus* recorded in the field during 1989–1993, between Cardwell and Townsville, are summarized in Fig. 1. In *M. perseus,* matings were recorded mostly in the afternoon and most frequently during the wet season-early dry season with an apparent peak in March-May. Very few pairs in copula were recorded during the late dry season (September-December). By contrast, *M. terminus* matings were recorded most frequently at midday, though the sample size was rather

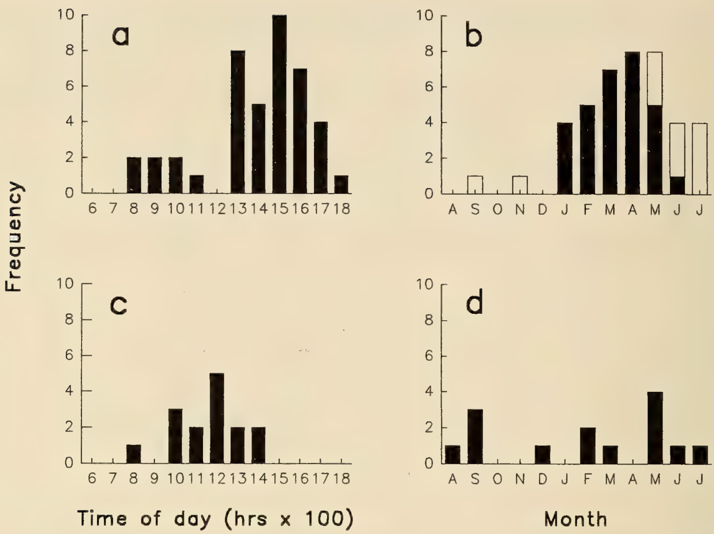

FIG. 1. Daily and seasonal variation in frequency of copulations in *M. perseus* (a, b) and *M. terminus* (c, d). Records are based on field observations accumulated for the period 1989–1993. Monthly records for *M. perseus* are divided into wet-season form (solid bar) and dry-season form (open bar).

small (n=15). The few matings recorded for *M. sirius* (n=11) precluded analysis of any daily or seasonal effects.

DISCUSSION

The relationship between mating frequency and age-class in Australian *Mycalesis* corroborates the findings of Lederhouse et al. (1989) for the tiger swallowtail *Papilio glaucus* Linnaeus in the United States. The three *Mycalesis* species are clearly polyandrous, but like *P. glaucus*, the frequency of mating increased significantly with wing-wear category, and a high proportion of virgins (>19% for each) was detected in the 'young' age-class (fresh category). Although the age of all females sampled was unknown, the assumption that wing-wear is broadly correlated with relative age is probably valid, although other factors such as inclement weather and predators may affect the quality of life, and hence wing-wear, to a certain degree (Lederhouse et al. 1989). However, it is noteworthy that significant (and similar) differences in mating frequency between *Mycalesis* were still evident once age affects were taken into account, although the differences persisted only among 'older' females.

The observations on diurnal and seasonal variation in mating observed in the field for *M. perseus* and *M. terminus* correspond well with their diurnal activity behavior and seasonal phenology (Braby 1995a, 1995b).

Both species have different peak activity periods during the day and they also show striking seasonal effects in mating state, particularly *M. perseus* in which spermatophore counts are highest during the breeding (wet) season. Hence, the effects of season and age are important variables in comparative studies. For example, it could be argued that *M. perseus* is strongly polyandrous, but only during its limited breeding period (Braby, 1995a), a finding which is not apparent when the count data are pooled for the two-year survey (Table 1 suggests *M. perseus* is only weakly polyandrous compared to *M. sirius*).

The effects of relative age (wing-wear) and season, together with the effects of spermatophore quality (size) (see Lederhouse et al. 1989) on mating frequency, underscore the need for caution when discussing the type of mating system favored by particular Lepidoptera (e.g., Ehrlich & Ehrlich 1978, Wiklund & Forsberg 1991). Only when these factors have been taken into account may it be reasonable to compare the mating strategies between species, or groups of species. If differences are found in insemination rate between species, or species groups, then adaptive explanations may be proposed.

Finally, why do older females tend to mate more frequently? Has the quantity of sperm from the first mating been insufficient to fertilize all eggs so that additional spermatophores are needed, or are females benefiting from male-derived nutrients, to enhance somatic maintenance and/or to increase reproductive effort? These questions may provide some fruitful areas of further investigation into the reproductive biology of Lepidoptera and the evolution of mating systems in general.

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FENNEL (*FOENICULUM VULGARE*), PRIMARY HOST PLANT FOR THE EASTERN BLACK SWALLOWTAIL (*PAPILIO POLYXENES ASTERIUS*) (PAPILIONIDAE) ON THE EASTERN SHORE OF VIRGINIA

Additional key words: life history, parasitoids, secondary plant chemicals.

The eastern black swallowtail, *Papilio polyxenes asterius* Stoll, is a common butterfly that occupies a wide variety of habitats such as fields, gardens, wastelands, and marshes. Its geographic range extends from Quebec west to Colorado and south to the mountains of northern South America (Opler & Malikul 1992). It is one of several species of the *machaon*-complex whose larvae feed primarily on plants in the subfamily Apioideae (Apiaceae = Umbelliferae) (Berenbaum 1981a).

Hosts of the black swallowtail include many plants in the family Apiaceae and a few plants in Rutaceae and Asteraceae (= Compositae) (Munroe 1960, Wiklund 1975, Berenbaum 1978, Scott 1986, Scriber & Finke 1978). Queen Anne's lace or wild carrot, *Daucus carota* (L.), is a common umbellifer on the Eastern Shore of Virginia. It grows along roadsides, in fallow fields, and in waste places throughout the eastern United States. Queen Anne's lace often has been reported as the primary host plant of the eastern black swallowtail (Scriber & Finke 1978, Blau & Feeny 1983).

Fennel, *Foeniculum vulgare* Miller, is a perennial plant in the Apiaceae. It has decompound leaves and filiform segments, with compound umbels of small yellow flowers; it blooms from June to September depending upon weather conditions. Fennel is known to be a host plant for the Old World swallowtail, *Papilio machaon* L., and the anise swallowtail, *Papilio zelicaon* Lucas (Berenbaum 1981b, Wiklund 1975, Scott 1986). It also has been noted by Stokes et al. (1991) and Ajilvsgi (1990) to be an occasional larval food plant for the eastern black swallowtail. On the Eastern Shore of Virginia, black swallowtails appear to use fennel as their primary host plant. Although both Queen Anne's lace and fennel commonly grow together, eggs, larvae, and ovipositing adults have been found only in association with fennel.

On the Eastern Shore of Virginia (Northampton County) fennel and Queen Anne's lace grow along most roads, pastures, and plowed fields. Both are very hardy and appear to persist under heavy disturbance. Fennel grows in thick clusters; mature plants reach heights of over 2 m. Queen Anne's lace grows in more diffuse patches that are usually spread out over a large area; mature plants reach heights of up to 1.5 m.

In October 1992, we first observed black swallowtail larvae feeding on fennel on the Eastern Shore of Virginia National Wildlife Refuge (ESVNWR). Twelve larvae were collected and returned to Virginia Commonwealth University (VCU) in Richmond, where they were fed fennel and exposed to an 8:16 (L:D) photoperiod. Pupae were placed in a constant temperature chamber at 4°C for winter. On 1 May 1993, the pupae were placed under a 16:8 photoperiod at a day/night temperature of approximately 24/18°C. After 15 days the first adult swallowtail emerged. Of the 12 larvae collected, two pupated but did not emerge, four emerged as healthy adults, and 6 pupal cases each contained a single parasitic wasp, *Trogus pennator* (Fabr.) (Hymenoptera: Ichneumonidae), a common parasite of swallowtail larvae/pupae (Heinrich 1962). One adult swallowtail and the wasps were saved and pinned as voucher specimens at VCU.

From September through November 1993, we collected over 30 black swallowtail larvae from fennel growing in the ESVNWR. No larvae were detected on Queen Anne's lace. Eighteen of the resultant pupae were allowed to diapause as described above. On 1 May 1994, pupae were placed at a day/night temperature of 24/18°C and exposed to a 16:8 L:D photoperiod. Adult eclosion began on 19 May. In all, six butterflies and eight *T. pennator* emerged; four pupa were dead. A summary of butterfly emergence and parasitism for 1992 and 1993 is shown in Table 1.

In September 1994, we searched fennel and Queen Anne's lace growing in the

TABLE 1. Fate of 30 *Papilio polyxenes asterius* Stoll larvae collected on the Eastern Shore of Virginia National Wildlife Refuge, 1992–93. All larvae pupated successfully; pupal parasitization was by *Trogus pennator* (Fabr.).

Year	Pupated	Died (%)	Eclosed (%)	Parasitized (%)
1992	12	2 (17)	4 (35)	6 (50)
1993	18	4 (22)	6 (33)	8 (44)
Totals	30	6 (20)	10 (33)	14 (47)

ESVNWR for black swallowtail eggs and larvae. Four females were observed ovipositing on fennel, and a total of 97 eggs and 42 larvae of various instars were collected from fennel. No black swallowtail eggs or larvae were observed on Queen Anne's lace despite the fact that this plant was abundant.

Our observations suggest that black swallowtails on the Eastern Shore of Virginia use fennel as their primary, and perhaps exclusive, hostplant. This utilization parallels the shift in host plant preference by the anise swallowtail, *Papilio zelicaon,* in coastal California. Increased abundance of *Papilio zelicaon* has occurred on the West Coast, and our preliminary data suggest that black swallowtail numbers are higher on the Eastern Shore of Virginia than in our study site in Chesterfield County, Virginia.

Host plant transfer to fennel could be deleterious to *P. polyxenes* larvae. Fennel contains furanocoumarins (Murray et al. 1982) which are toxic to most phytophagous insects. However, xanthotoxin enhances *P. polyxenes* larval growth (Berenbaum 1981b). In our laboratory, larvae pupated and adults emerged and subsequently deposited viable eggs when reared on fennel. Both fennel and wild carrot occur in great abundance on the ESVNWR. We have counted over a thousand plants of each species within a 20 m^2 plot. The excessive numbers of each in various stages of development during the entire April-November growing season precludes oviposition selection due to population density alone. It is known that wild carrot is less attractive for oviposition in the fall (Feeny et al. 1985); however, we have observed both oviposition and larval feeding only on fennel throughout the April-November season at the ESVNWR.

The shift of *P. zelicaon* to fennel in coastal California may be due to the presence of palatable foliage throughout the summer. Most of the native umbellifers are in leaf and/or flower only in the spring or fall due to the Mediterranean climate which includes dry, hot summers. We suggest that the shifts in host plants reported for *P. zelicaon* and *P. polyxenes* could have a chemical basis (e.g., fennel may contain larger quantities of an oviposition stimulant such as luteolin-7–0-(6'-0-malonyl)-B-D-glucoside (Feeny et al. 1988)).

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FIFTH INSTAR PARASITOIDS OF *ANAEA RYPHEA* (NYMPHALIDAE): THE MISSING DATA

Additional key words: population ecology, pupal mortality, Tachinidae.

In two previous articles, I described the life cycle of *Anaea ryphea* Cramer (Caldas 1994) and the population ecology of its immatures (Caldas 1995). These studies were conducted at Campinas, Brazil (22°54'S, 47°05'W, 650 m elevation) and included results on larval and egg parasitoids. However, I failed to identify mortality factors acting on fifth instar larvae and pupae, because preventing fifth instar larvae from leaving the foodplant for pupation might have influenced the number of future adults within that population, and therefore the study that was being carried out (see Caldas 1995 for details). To remedy this situation, after finishing the population studies, I decided to look for pupal and fifth instar parasitoids.

I collected 15 fifth-instar larvae of *A. ryphea* on plants of *Croton floribundus* Spreng (Euphorbiaceae) in late May 1994 at Itatiaia National Park in Rio de Janeiro state, Brazil (22°27'S, 44°37'W, 800 m elevation), a reserve about 300 km east of Campinas. I kept larvae in large plastic vials, and fed them until pupation. Eight individuals, immediately after pupation (less than 24 hours), started turning dark, eventually turning into a deep brown, whereas the other seven kept their typical bright green color. After 10-12 days, maggots emerged from four of the dark pupae (one maggot from each pupa), and immediately tried to pupate on the vial bottom. Only two pupated successfully. Adults were identified as a female of *Winthemia* Robineau-Desvoidy (Diptera: Tachinidae) and a female of *Jurinella* Brauer & Bergenstamm (Diptera: Tachinidae). Unfortunately, no males

emerged, which made specific identification impossible. The parasitoids inside the four other *A. ryphea* pupae also failed to pupate.

Although a sample size of 15 larvae is not large enough for definitive conclusions, the rate of parasitism reported here on fifth instar larvae of *A. ryphea* (53%) is as high as the rate of egg parasitism by trichogrammatid wasps (55%) and the rate of mortality in first instar larvae (49%, on average). Larval behaviors, such as leaf rolling and nocturnal feeding in fourth and fifth instar larvae, may decrease the incidence of parasitism, but it would appear that mortality due to parasitism during fifth larval instar may affect the population size of *A. ryphea* just as much as that during the earlier life history stages.

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VARTIAN COLLECTION TO THE MUSEUM OF NATURAL HISTORY, VIENNA

Additional key words: Noctuidae, type specimens, palaearctic.

The Museum of Natural History in Vienna recently received the Eva Vartian collection of western and southern Palaearctic Macrolepidoptera. The value of the collection is extraordinary, and its strength results from the extensive entomological field work conducted by Mrs. Vartian in the Near and Middle East. The collection contains all groups of Macrolepidoptera, and is dominated by Noctuidae and Geometridae. The breadth of the collection is unusual: among the Noctuidae, for example, are more than 2,500 type specimens, with rich representation in the subfamilies Noctuinae, Hadeninae, Cuculliinae and Amphipyrinae. Overall, the collection is estimated to contain a total of 4,400 type specimens, some hundreds of which are holotypes.

About 95 percent of the 140,000 specimens are set and housed in more than 900 drawers. The entire collection is presented in its own room, the "Vartian Hall," situated on the top floor of the building. A large part of the material was collected by Mrs. Vartian during dozens of expeditions to Turkey, Iraq, Iran, Afghanistan and Pakistan. In combination with the rich western Palaearctic material already extant in the main collection, and the collections of Rudolf Pinker (Northern Africa, Turkey), the Museum of Natural History in Vienna now has one of the largest Macrolepidoptera and especially Noctuidae collections for the Near and Middle East in the world.

Lepidopterists who expect to be in Austria may visit the Museum of Natural History in Vienna and examine the collection by prior arrangement. Please contact Dr. Martin Lödl at the address below (Tel. 0043 (1) 521 77 ext. 318).

MARTIN LÖDL, *Naturhistorisches Museum Wien, 2. Zoologische Abteilung, Burgring 7, A-1014 Wien, Austria.*

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50(1), 1996, 92–95

OBITUARY

ALEXANDRE CONSTANTINOVICH CHNÉOUR (SCHNEEUR) (1884–1977)

Alexandre Constantinovich Chnéour, a very enthusiastic avocational lepidopterist and herpetologist, was born in St. Petersburg, Russia, on 30 August 1884. When publishing in German in the 1930s, he used "Schneeur" for his surname. I was informed that his name is of German origin. Between 1934 and 1963 he published on the Macrolepidoptera of Tunisia, and he was especially interested in their zoogeography. He died in his 93rd year, on 16 September 1977, at the Laguna Honda Hospital, in San Francisco, California, after some years of declining health.

Alexandre Chnéour told me that he became interested in butterflies as a boy, and as a young man he travelled to Germany and Switzerland. In St. Petersburg he attended the private Gurevich Middle School and then applied and was accepted into the Mihailovsky Artillery School. Upon graduation, with the rank of lieutenant, he entered service as an officer of a horse artillery unit. During the First World War he distinguished himself and was awarded several battle decorations. In 1916 he was transferred to the Russian Air Force, completed a two month long course in the Kiev School for Observers, and started a brief career in aviation. He also attended wartime accelerated studies in the Academy of the General Staff, and graduated in February 1917.

During the Civil War in Russia between 1917 and 1922, he joined the ranks of the White Anti-Communist "Volunteer" Army, as opposed to the Red Communist Army, and he fought the Reds mostly in the Caucasus region. After the end of this struggle he was evacuated with others from Russia to the Gallipoli Camp in Turkey. He then moved to Bulgaria where he was a lecturer in the Officers Engineering School, lecturing to the still remaining organized Russian Army Units (in both this and in the former camp in Turkey).

Alexandre Chnéour then found refuge in Lyon, France. In 1929 he moved to Tunisia, which was then a French colony, as a member of the French Geographical Department, working as a draftsman for the Department of Roads and Bridges. He resided in Tunis until Tunisian independence in 1956 forced his move. He was admitted as an immigrant to the United States on 2 June 1956. He lived at first in the New York City area, and he studied at the American Museum of Natural History in 1961 verifying his Tunisian identifications. In 1963, Chnéour published in French a resumé of his Lepidoptera work in Tunisia, with the translated title of "Twenty-six years of work of a lepidopterist in Tunisia," which covered the years from 1930 to 1956.

In 1934 Chnéour commenced publishing on the Tunisian lepidopteran fauna, beginning with six papers published in German in German journals under the name "Schneeur" (between 1934 to 1937), followed by fourteen papers in French (from 1942 to 1963) primarily in Tunisian journals. He was also very helpful to Soures in his study of the harmful Lepidoptera of Tunisia (Soures 1950), and is so acknowledged and the California Academy of Science's copy of the publication is dedicated "A M. Chneour, l'Eleve à son Maitre. l'auteur reconnaissant, Soures." Alexandre Chnéour was also interested in the herpetofauna of Tunisia and coauthored a study of "Les Serpents de Tunisie" (Chpakowsky & Chnéour 1954).

Rindge (1967:180) reported that Chénour's primary collection of Tunisian Macrolepidoptera, consisting of 806 specimens, including primary types of 11 taxa (four Pieridae, four Satyridae, one Noctuidae, and two Lasiocampidae), had been donated to the Lepidoptera collection of the American Museum of Natural History. In a summary article on his Lepidoptera studies in Tunisia, Chnéour (1963:109) reported 603 species of Macrolepidoptera in his collection, in contrast to only 93 taxa of Microlepidoptera. He stated that the low number of the latter was due to specialists who still had his specimens out on loan. These microlepidopterans probably must still exist in various collections in western Europe. Chnéour donated 415 specimens to the California Academy of Sciences, which were accessioned between 17 June 1964 and 20 May 1969, including at least five North African Satyridae, with one labeled as paratype of *Satyrus colombati stellifer* Chnéour.

Alexandre Chnéour's longest entomological association was with the Société entomologique de France, becoming a member in 1942. When in the United States, he became a member of the Lepidopterists' Society and is listed in the 1964 (Downey 1964:8) and 1967 (Downey 1967:9) membership lists.

In San Francisco, Alexandre Chnéour resided at 1830 Divisadero Street. In his latter 80s this gentleperson was viciously mugged while entering his apartment, and required hospitalization. His last years were spent as a resident of the Laguna Honda Home and Hospital. At the time of his death Alexandre Chnéour was survived by his sister-in-law Mrs. Tatiana Miller, who told me of his wish that I notify the Société entomologique de France of his death after that occurred. His third wife Elizabeth (née Tirnstein) died in San Francisco in 1971.

I acknowledge the assistance of the following individuals who provided information and/or editorial assistance: Veronica Ahrens-Pulawski, Tatiana Miller, and Valeree Milanovanovich Tomitch of San Francisco; Nicholas Zakharoff of San Vito, Costa Rica; Ron Leuschner of Manhattan Beach; Frederick H. Rindge, American Museum of

Natural History; and at the California Academy of Sciences, Lawrence W. Currie, Jr. and Patty Shea-Diner of the J. W. Maillard Jr. Library, and Madeline M. Arnaud, Helen K. Court, and Vincent F. Lee of the Department of Entomology. John Tennent's (of Flyingthorpe, Whitby, North Yorkshire) inquiry for information on Alexandre Chnéour (Tennent 1994:99) instigated the preparation of this article, and he also provided information. A more detailed account on Alexandre Chnéour will be published in volume six of the publication *Myia*. No portrait of Alexandre Chnéour is currently available.

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1934. Die Tagfalter von Mittel-Tunis. Entomol. Zeit. Frankfurt-M. 48:36–37, 41–46. ["Von A. Schneeur."] [*Papilio machaon chrysostoma* Chnéour, new form; *Euchloe belemia marmorata* Chnéour, new form; *Leucochloe daplidice hiberna* Chnéour, new form.]

1935a. Beschreibung einer neuen Aberration von *Satyrus abdelkader* Pier. Entomol. Zeit. Frankfurt-M. 48:190–191. ["Von A. Schneeur, Tunis."] [*Satyrus abdelkader marteni* Chnéour, new aberration.]

1935b. Eine neue Form von *Euchloë falloui* All. Entomol. Zeit. Frankfurt-M. 49:49. ["Von A. Schneeur, Tunis."] [*Euchloe falloui choumovitschi* Chnéour, new form.]

1936a. Einige Bemerkungen nebst Verbesserungen über das Werk Bodo v. Bodemeyers "Ueber meine entomologischen Reisen" und der merkwürdigen verbreitungsgrenze der Falter in Nord-Afrika. Entomol. Zeit. Frankfurt-M. 49:480–481. ["Von A. Schneeur, Tunis."]

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1942a. Contribution à l'étude des macrolépidoptères de Tunisie. Bull. Soc. Hist. Nat. l'Afrique du Nord 33:43–58. [*Satyrus colombati stellifer* Chnéour, new aberration; *Satyrus statilinus Chpakowskyi* Chnéour, new subspecies; *Lasiocampa trifolii Lutzernowi* Chnéour, new aberration.]
1942b. Une nouvelle hétérocère trouvée en Tunisie: *Simyra Chpakowskyi* nov. spec. (Lep. Noctuidae). Bull. Soc. Hist. Nat. l'Afrique du Nord 33:86–87. [*Simyra Chpakowskyi* Chnéour, new species.]
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1950b. [Description of *Lasiocampa trifolii Chpakowskyi* Chnéour, new subspecies.], pp. 150–151, *In* Soures, B., Contribution à l'étude des Lépidoptères de la Tunisie. Biologie des espèces nuisibles ou susceptibles de le devenir. Ann. Ser. Bot. Agr. Tunisie (1948), 21. [*Lasiocampa trifolii Chpakowskyi* Chnéour, new subspecies.]
1952. Contribution à l'étude des macrolepidoptères de Tunisie. Bull. Soc. Hist. Nat. l'Afrique du Nord (1950) 41:41–47. [*Pieris rapae minor Nana* Chnéour, new variety; *Satyrus sylvicola Cordieri* Chnéour, new variety [should have been *cordierae* since it was named after "Mlle Cordier, Docteur de l'Institut Arloing de Tunis"]; *Erias insulana Bedei* Chnéour, new variety.]
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SOME PATRONYMS HONORING ALEXANDRE CHNÉOUR

Capitalization of new taxa is given as originally proposed, with the type locality at the end of each citation.

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Crambus Chnéouri Lucas, 1942:122. Tunisia: Protoille et Sbeïtla.
Moenas chneouri Rungs, 1951:99–101. Tunisia: Sbeïtla.
Mymecozela Chnéouri Lucas, 1942:126. Tunisia: Sbeïtla.
Tephris chnéourella Lucas, 1946:97. Tunisia: Nefta.
Tineola chnéourella Lucas, 1951:143. Tunisia: Maknassy.

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MANUSCRIPT REVIEWERS, 1995

The merit of a scientific journal depends on the quality of its reviewers as well as of its authors, but the former are usually unknown to readers. The *Journal* relied on the expertize of 58 reviewers last year to provide 91 evaluations of manuscripts. It is with much gratitude that the *Journal* acknowledges the services of the people listed below from whom manuscript reviews were received in 1995. Those who reviewed two or more manuscripts are denoted by asterisks.

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SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.
——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

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CONTENTS

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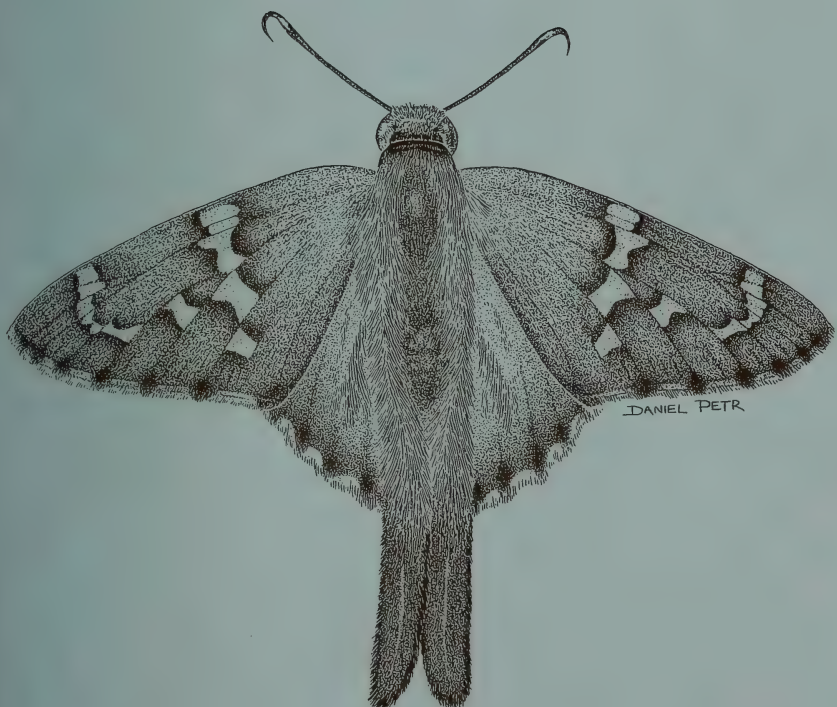

5 July 1996

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The object of the Lepidopterists' Society, which was formed in May 1947 and formally constituted in December 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

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Cover illustration: *Urbanus proteus* (Hesperiidae), a skipper denizen of Jalisco, Mexico (see article inside by Vargas et al.). Original pen and ink drawing by Daniel Petr, Department of Biology, Southwestern Adventist College, Keene, Texas 76059.

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BUTTERFLIES OF THE STATE OF JALISCO, MEXICO

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ABSTRACT. A survey of the butterflies of the state of Jalisco, Mexico is presented, in which 608 species from 309 genera and 22 subfamilies of Papilionoidea and Hesperioidea are listed, from 190 localities. Many species are reported from Jalisco for the first time, including one skipper, *Vacerra cervara*, that is new to Mexico. This list was created by reviewing the past Lepidoptera literature and the major collections in the United States and Mexico, as well as through field work at 10 sites carried out by the authors. For each species, capture localities, adult flight dates, and references for the data are provided. Species richness is analyzed for the Mexican states of Baja California (north), Baja California Sur, Jalisco, Guerrero, Veracruz, Oaxaca, Chiapas, and Quintana Roo.

Additional key words: biogeography, conservation, distribution, Hesperioidea, Papilionoidea.

RESUMEN. Se integró el listado de los ropalóceros del estado de Jalisco, el cual consta de 608 especies, pertenecientes a 309 géneros y 22 subfamilias de Papilionoidea y Hesperioidea. Se registraron 190 localidades para todo el estado. Se mencionan nuevos registros para Jalisco, incluyendo *Vacerra cervara*, que es nueva especie para México. Este listado se formó a partir de la revisión detallada de la literatura publicada sobre Lepidoptera y de las principales colecciones de los Estados Unidos y México, así como del trabajo de campo efectuado por los autores en diez sitios en el estado. Se citan para cada especie las localidades y fechas de recolecta y la referencia de éstas. Se comparó la riqueza de especies de Jalisco, con la de otros estados como Baja California (norte), Baja Califronia Sur, Guerrero, Veracruz, Oaxaca, Chiapas y Quintana Roo.

Palabras clave adicionales: biogeografía, conservación, distribución, Hesperioidea, Papilionoidea.

This work constitutes the first in a series of papers on the butterflies of the states of western Mexico: Sinaloa, Nayarit, Jalisco, Colima and Michoacán. As in previous similar studies by the Mexican authors on the butterflies of the Valley of Mexico (Luis & Llorente 1990), and the

states of Guerrero (Vargas et al. 1994) and Oaxaca (Luis et al. 1991), each work in this series is based on intensive field studies carried out in the most species-rich and biologically, geographically, and climatically diverse areas in each Mexican state, the compilation of distributional data from specimens in the major lepidoptera collections in Mexico and the United States, and a thorough review of the Lepidoptera literature.

With data from over 100,000 Mexican butterfly specimens obtained during field studies in ten states of the Mexican Republic (at the "Alfonso L. Herrera" Zoology Museum at U.N.A.M.), combined with data from about 40,000 specimens in American collections, and about 90,000 specimens in other Mexican collections, we are in the process of forming a large cross-referenced database of Mexican butterfly localities and all the butterfly species known from them, which will be useful for biogeographical and conservation studies. Using geographical information along with the distributional information in the database, it will be possible to plan better strategies for conducting faunal surveys on butterflies in Jalisco, or any other Mexican state, in the future. Until recently, there have been few faunal works conducted on butterflies in Mexico. However, it is essential to advance our knowledge of the geographical distribution of butterflies in Mexico in order to generate effective conservation criteria, for we know that butterflies can be excellent ecological and biogeographical indicators.

This work presents the distributional information known so far for each butterfly species recorded from the state of Jalisco. This work was developed in order to make available to researchers and naturalists the preliminary knowledge of the distribution of each butterfly species recorded in Jalisco to date. Researchers studying any species or group of butterflies will now have reference to what is known about their taxa in Jalisco, and eventually, in all of western Mexico. This work also stresses the need for continued studies on the butterflies of Jalisco, and will provide a knowledge base from which future studies may benefit.

ANTECEDENTS

The earliest formal studies treating Mexican butterflies are *Biologia Centrali Americana* by Frederick du Cane Godman and Osbert Salvin (1879–1901), and *Die Gross Schmetterlinge der Erde* (*The Macrolepidoptera of the World*) by Seitz (1924). It was in these works, principally in that by Godman & Salvin, where we see the first attempts at regionalization of the Mexican butterfly fauna, considering political divisions, geographical units, altitudinal intervals, and vegetational aspects. Godman and Salvin cited 81 species for Jalisco (33 Papilionoidea and 48 Hesperioidea). Only five localities were mentioned for butterflies in Jalisco: Bolaños, Chapala, Guadalajara, Lago de Chapala, and "Jalisco".

In 1940 (published again in 1976, as cited below), after over 40 years of research, Carlos Christian Hoffmann published his *Catálogo Sistemático y Zoogeográfico de los Lepidópteros Mexicanos.* Hoffmann reported 1,240 species of butterflies from Mexico, citing 76 for the state of Jalisco (47 Papilionoidea and 29 Hesperioidea). Additionally, 180 species are inferred for Jalisco in citations he made, including: "Pacific Region from Chiapas to Sinaloa," "Sierra Madre Occidental," "everywhere in the country," "south and both coasts," and "western region." Hoffmann's catalog was based partly on the previous works by Godman and Salvin, Seitz, and articles published during the first three decades of this century. Collections consulted for his catalog included those of Roberto Mueller and Tarsicio Escalante, as well as his own (Hoffmann's collection is now deposited in the American Museum of Natural History, New York, and Escalante's collection is at the Allyn Museum of Entomology, Sarasota, Florida).

In the following four decades (approx. 1940–1980), there was little study on butterflies in the state of Jalisco. Escalante continued some fieldwork in Jalisco in the late 1940s, especially around Cihuatlán and Ameca. In about 1960, John Adams Comstock and Leonila Vázquez spent a year in Puerto Vallarta rearing many species to obtain life history information. Other principal workers who collected in Jalisco during these years include: Don B. Stallings and J. R. Turner (who collected around Guadalajara, 1957), Robert Wind (mostly at Atenquique and Ajijic, 1965–1967), Peter Hubbell (mostly at Coastecomate Bay, La Cumbre de Autlán, Río San Pedro, Mirador, and near Sayula, 1966–1968), and Lee D. and Jacqueline Y. Miller (who collected near Magdalena in 1973). There are also some specimens scattered throughout museum collections collected during these years from "Puerto Vallarta" by vacationing tourists to the area.

In 1987, after many years of collecting butterflies in Mexico, Roberto De la Maza Ramírez published *Mariposas Mexicanas.* In this book he illustrated more than 600 species of butterflies, mostly species endemic to Mexico, and with very localized distributions that are difficult to catch and observe. His book represents the most complete work on Mexican butterflies presented since Hoffmann's, and in it only 64 species are cited from 15 localities in Jalisco.

STUDY AREA

The state of Jalisco is situated in the western region of the Mexican Republic between the parallels of 18°58′00″ N and 22°45′00″ N and 101°27′40″ W and 105°41′25″ W. Jalisco occupies an area of 80,137 km^2, which constitutes 4.1% of Mexico's total surface area. The Pacific shoreline extends 345.9 km, from the Ameca River in the north, to the Mar-

abasco River in the south. Fourteen types of vegetational life-zones are found in Jalisco: high mountain prairie, Oyamel forest, cloud forest, oak forest, pine-oak forest, pine forest, *Juniperus* forest, *Juniperus* scrub, tropical semi-deciduous forest, tropical deciduous forest, thorn forest, subtropical chaparral, alkaline flats, and mangrove. Jalisco ranks sixth among the Mexican states in overall terrestrial vertebrate diversity, according to Flores and Gerez (1988).

Jalisco currently has eight protected areas, two of which are scientific stations (Chamela Biological Station, U.N.A.M., and Las Joyas Natural Laboratory, University of Guadalajara); one National Park combined with parts of the state of Colima (Nevado de Colima Volcano), four beach refuges for marine turtles (Playa Cuitzamala, El Tecuán, Mismaloya, and Teopa); and one Biosphere Reserve in the Sierra de Manantlán where *Zea diploperennis* (perennial corn) was first discovered.

MATERIALS AND METHODS

Collections and Literature. This listing of butterfly species known from Jalisco, which has taken ten years to compile (1984–1994), includes the species of butterflies reported from Jalisco in the past Lepidoptera literature (see Literature Cited), as well as the specimen locality data from Jalisco butterflies in the major Lepidoptera collections in the United States and Mexico. The data from all Mexican specimens in major collections in the United States and Mexico is organized in a computerized database at the "Alfonso L. Herrera" Zoology Museum at U.N.A.M., which greatly facilitated the retrieval of locality information for this list.

Not every Jalisco specimen cited in the literature by researchers (including foreign and Mexican collectors), was examined by us in this study. Such a complete revision of past collections would have drawn this work out indefinitely. Very little Jalisco material from the De la Maza collection, for example, was examined, although we have some Jalisco citations from literature by the De la Maza's. The following is an alphabetical list of the abbreviations used for the museums and collections examined that contained Jalisco material: **ADW** = recorded by Andrew D. Warren, includes Warren (1991, 1993, 1995b); **AME** = Allyn Museum of Entomology (Sarasota, FL); **AMNH** = American Museum of Natural History (New York City, NY); **BMNH** = British Museum of Natural History (London, England); **CAS** = California Academy of Sciences (San Francisco, CA); **CIB** = Entomology Collection in the Institute of Biology, U.N.A.M. (Mexico City); **CMNH** = Carnegie Museum of Natural History (Pittsburgh, PA); **COEE** = Entomology Collection at the Office of Special Studies, S.A.G. (Mexico City) (see Gibson & Carrillo 1959); **CUIC** = Cornell University Insect Collection

(Ithaca, NY); **DGSV** = Dirección General de Sanidad Vegetal (see Hernández et. al. 1981); **IMCyP** = Institute of Wood, Fiber, and Paper, University of Guadalajara (Guadalajara, Jalisco) (see Abud 1987, 1988); **LACM** = Los Angeles County Museum of Natural History (Los Angeles, CA); **MZFC** = "Alfonso L. Herrera" Zoology Museum, Faculty of Sciences, U.N.A.M. (Mexico City); **RES** = recorded by Ray E. Stanford (Denver, CO).; **SDNHM** = San Diego Natural History Museum (San Diego, CA); **UCB** = Essig Museum of Entomology, University of California (Berkeley, CA); **USNM** = United States National Museum, Smithonian Institution (Washington, D.C.).

Literature and non-literature source citations almost always refer to actual specimens, but we have included a few positive sight records from our personal notes that are not backed up by specimens (including very few ADW and MZFC records), and Opler's (1989) list of species from Chamela is based on photographs (determined by Warren) and sight recordings. Other literature records may or may not be backed up by specimens. The citation "Freeman unpubl." in the species list refers to an undated 142 page manuscript by Hugh Avery Freeman entitled "The distribution of Hesperiidae in Mexico."

Only five major faunistic studies on butterflies (of more than about one week in duration) in Jalisco have been reported in the literature: the year of life history studies by J. A. Comstock and L. Vázquez (1961) in Puerto Vallarta; the list of species found by Beutelspacher (1982b) at the U.N.A.M. Biological Station at Chamela; the work by S. Rodríguez (1982) at Acatlán de Juárez; the works by Abud (1987, 1988) in the Spring Forest near Guadalajara; and the work by G. A. López (1989) in the Huentitán area near Guadalajara. As with the majority of past faunistic studies on butterflies in Mexico, most of the past studies in Jalisco presented a surprisingly low number of butterfly species, for the field work in these studies was not based on a systematic methodology with surveys throughout the year, as described by Luis et. al. (1991). Faunal studies on Mexican butterflies in other states, such as De la Maza and Gutiérrez (1992) for Quintana Roo, Brown et. al. (1992) for Baja California, and De la Maza and De la Maza (1993) for Chiapas were used for Table 1.

Many sources were consulted in determining the nomenclature in the species list, including the original descriptions for all species described from Jalisco. Many additional species-group or generic revisions were reviewed for nomenclatural purposes, and for additional locality data. A few works that were reviewed which did not contribute locality data for Jalisco (and therefore may not be cited in the species list), but were used primarily for nomenclatural reasons include: Bailowitz (1988), Bridges (1993), Brower (1994), Burns (1964, 1992a, 1992b,

1994a, 1994b), Callaghan (1983), De la Maza and Díaz (1979), De la Maza et al. (1989), DeVries (1987), Fox & Real (1971), Friedlander (1987), Harvey (1991), Jenkins (1985), Lamas (1979), Llorente (1984), Llorente and Garcés (1983), Llorente et al. (1990), Mielke (1994), and Tyler et al. (1994).

Field Work. The majority of the localities and records presented here are from the field work carried out over the past three years by us in the Sierra de Manantlán, totaling 87 days in the field (three persons participating); and the work carried out over the past six years in the Banderas Bay Region (Puerto Vallarta to Boca de Tomatlán) by Andrew Warren, totaling about 33 days (one or two persons participating). In the Sierra de Manantlán, collecting was done between altitudinal extremes from 300–2200 m in three main life zones: semi-deciduous tropical forest, deciduous tropical forest, and cloud forest. A detailed analysis of the distribution of the Papilionoidea of this area is currently under way (Vargas et al. unpubl.). Most field work done in the Banderas Bay area was from 0–200 m elevation, in deciduous tropical forest, but some surveying was done in pine-oak forest and thorn forest habitats as well.

RESULTS

Based on our review of collections, publications, and field work carried out to date, we have obtained a list of 608 species, in 309 genera, of 22 subfamilies in the superfamilies Hesperioidea and Papilionoidea from Jalisco. In this list, many species are reported from Jalisco for the first time, and one skipper, *Vacerra cervara* Steinhauser, is reported for the first time from Mexico. We have examined material from 190 localities in Jalisco, of which 70% are represented by five or fewer species. This shows that there is still a generally poor knowledge of the distribution of butterflies in this state.

The areas of the state with the greatest observed butterfly diversity are shown in Fig. 1. Of the ten richest sites, four are from the faunistic work being carried out in the Sierra de Manantlán (La Calera, Ahuacapán, Zenzontla, and Puerto Los Mazos), and four others refer to work carried out around Banderas Bay (Mismaloya, Puerto Vallarta, Boca de Tomatlán, and Río las Juntas near Chico's Paradise). We also have a substantial number of literature and museum records for La Calera, Mismaloya, Puerto Vallarta, the Chamela area, and Barranca de Huentitán. The four localities studied in the Sierra de Manantlán, which have been researched systematically by members of the Zoology Museum (MZFC), have yielded 353 species, including 58% of the Papilionoidea known from the state. The majority of the species cited in this list are from only three areas in the state: the Sierra de Manantlán, the coastal

and montane areas around Puerto Vallarta, and the montane habitats near the city of Guadalajara (see Fig. 1).

As mentioned by Luis et al. (1991) there have been few faunistic studies of Mexican butterflies in the past, and those that have been made often do not express the true butterfly diversity present at the study sites. For example, Opler (1989) reported 85 species from Estación de Biología Chamela, UNAM, from a one day list, and several of the species he reported (especially skippers) were not found in Beutelspacher's 1982 list of Chamela butterflies. Only in the last decade have rigorous, formal faunistic studies on Mexican butterflies been caried out with a systematic method. However, information on the geographical distribution of butterflies in each Mexican state is still incomplete (there is little or no distributional information available on butterflies for some states e.g., Tlaxcala). In Table 1, states are listed for which we have a more or less "complete" list of species, based on our own collecting, complemented in most cases by records from the literature and from museum collections. Table 1 shows that the state with the greatest diversity of butterflies is Chiapas, with a current total of 1,194 species, followed by Veracruz with 714 species (not including Hesperioidea, probably around 450 additional species). The states in Baja California apparently have the smallest number of butterfly species. Although fewer than 100 species have been recorded from Coahuila (Stanford & Opler 1993), no rigorous faunistic studies have been made in that state, and the number is certainly much higher.

Of the 608 species of butterflies reported here for the state of Jalisco, the majority are known mostly from the ten localities marked on Fig. 1. Since most of the now available data on Jalisco butterflies is from these ten localities, the total number of butterfly species that actually occur in Jalisco is undoubtedly considerably higher (probably at least 35 additional Hesperioidea alone). Many species that have been recorded to the north in Nayarit, and to the south in Colima and Michoacán (such as *Pyrrhophyge araxes* (Hewitson) and *Phocides urania urania* (Westwood), to name just two of the skippers), will undoubtedly be found in Jalisco with further field work. There are vast regions of Jalisco, especially in the northern and north-eastern parts of the state, for which we have practically no butterfly records. This map and list help to demonstrate that the Jalisco specimens deposited in Mexican and foreign collections express only a limited knowledge of the geographical distribution and diversity of butterflies for the majority of the state. Clearly, in order to attain a more complete knowledge of the distribution of butterflies in Jalisco, more field work in the unexplored regions is needed.

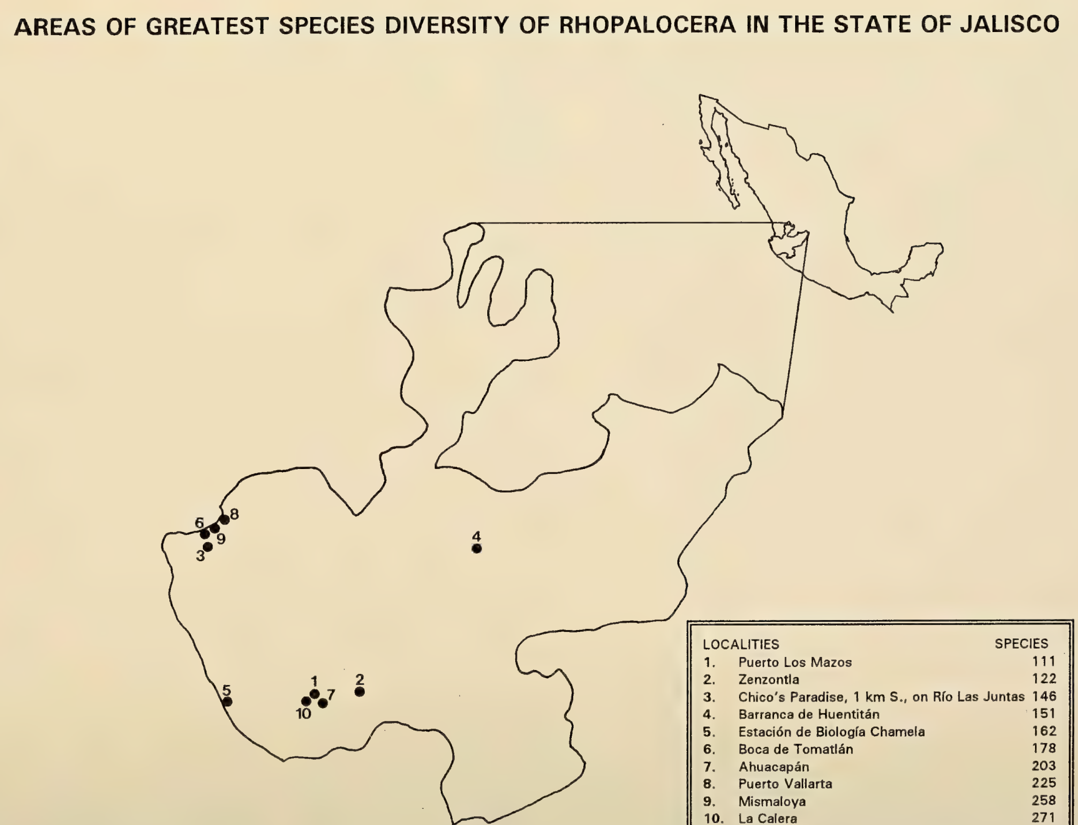

FIG. 1. Areas of greatest species diversity of Rhopalocera in the state of Jalisco.

TABLE 1. Species counts by lepidopteran family for Mexico. State abbreviations and sources used are: BC = Baja California (norte) (Brown et al. 1992); BCS = Baja California Sur (Brown et al. 1992); JAL = Jalisco (this paper); GUE = Guerrero (Vargas et al. 1994); VER = Veracruz (Luis et al. unpubl.); OAX = Oaxaca (Luis et al. 1991); CHI = Chiapas (De la Maza & De la Maza 1993); QRO = Quintana Roo (De la Maza & Gutiérrez 1992). Asterisks indicate numbers that are still incomplete, and are not included in the state totals.

	BC	BCS	JAL	GUE	VER	OAX	CHI	QRO
Papilionidae	6	4	28	36	41	47	43	23
Pieridae	20	21	43	47	56	57	57	27
Nymphalidae	26	24	158	213	297	318	352	122
Lycaenidae	45	26	136	190	320	162	307	93
Hesperiidae	39	35	243	*	*	*	435	118
Totals	136	110	608	486	714	584	1194	383

BUTTERFLIES OF JALISCO

The format of this list was designed to include the maximum amount of information in as little space as possible, and still be easy to read and use. Following each species name are the localities where it has been recorded in Jalisco, roughly in alphabetical order. Locality data pertaining to the same general area, such as "Bahía de Chamela," and "Estación de Biología Chamela, UNAM" are listed together, despite their non-alphabetical order, to avoid confusion. Localities that occur more than 20 times throughout the list are presented as 3–4 letter capitalized abbreviations (see Table 2).

Following each locality are the months (in lowercase Roman numerals) the species has been found at that locality. For several literature records, no months of capture were available. Each locality, or series of localities and dates, is followed by a source for the record(s). The sources are either capital letter abbreviations for personal records and museum collections (see Materials and Methods), or a literature citation (author and date). If no source is listed directly after a locality or month, the next source listed (it may be after several additional localities and months) pertains also to the first source in the series. If for a species, only one source is given after several localities and months, all the records are from the one source listed. When one locality for a single species has appeared in several publications, the cited publication is either the most authoritative for that species (generic or species-group revision), or the earliest dated publication in which the record appeared, when no generic revision is available. Occasionally, two non-revision literature citations are provided for one locality. When we have three or more sources for a single locality record, it is followed by "(many)." When literature records are available for the same specimens that have been examined in Museums, the literature citation may or may not be given, but the museum citation usually is. For some species, we have no specific locality records, and only a general "Jalisco" (JAL) record is listed. These are species that have been recorded from Jalisco by other workers, and no exact locality data could be determined.

As an example of how to read the entires, refer to the first species, *Pyrrhopyge chalybea*. The passage says: López (1989) reported it at Barranca de Huentitán (BDH) from February to April; specimens from Guadalajara (GUA) from July, September, and October are in the British Museum of Natural History; Guadalajara specimens from June are in the Allyn Museum of Entomology; Guadalajara specimens from March are in the American Museum of Natural History; and specimens labeled from "Jalisco" (JAL) from July are in the BMNH and the Cornell University Insect Collection.

HESPERIIDAE (243 SPECIES)

Pyrrhopyge chalybea (Scudder 1872). BDH ii–iv (López 1989); GUA vii,ix,x (BMNH), vi (AME), iii (AMNH); JAL vii (BMNH, CUIC).

TABLE 2. Abbreviations used in the species list for the 35 most commonly cited Jalisco localities.

Abbreviation	Locality
ADJ	Acatlán de Juárez
AHU	Ahuacapán
AJI	Ajijic
BDH	Barranca de Huentitán
BDN	Barra de Navidad
BDT	Boca de Tomatlán
BES	Bosque Escuela, de la Sierra de la Primavera
BHC	Bahía Coastecomate
BOL	Bolaños
CHI	Chico's Paradise
CHIS	Chico's Paradise, 1 km S on Río Las Juntas
CHM	Chamela
CHP	Chapala
EBC	Estación de Biología Chamela, UNAM
EC	Estación Científica, Las Joyas
ECAL	Estación Científica, Las Joyas, Almeal
ECET	Estación Científica, Las Joyas, El Triguito
ECLC	Estación Científica, Las Joyas, La Cascada
ECLO	Estación Científica, Las Joyas, La Ordeñita
ECPE	Estación Científica, Las Joyas, Puerto Escobedo
ELT	El Tigre
GUA	Guadalajara
JAL	"Jalisco"
LCA	La Calera
LCU	La Cumbre de Autlán
LDC	Lago de Chapala
MAG	Magdalena
MIS	Mismaloya
PLM	Puerto Los Mazos
PV	Puerto Vallarta
RT	Río Tomatlán
TEN	Tenacatita
YEL	Yelapa
ZEN	Zenzontla

Pyrrhopyge chloris Evans 1951. AHU vi (ADW); AJI viii,ix (AMNH); BDT xii; LCA vi; MIS xii; PV xii (ADW).

Elbella scylla (Mén. 1855). AHU vi; BDT i; LCA vi (ADW); PV (Comstock & Vázquez 1961).

Mysoria amra (Hewit. [1871]). BDT xii (ADW); Bahía de CHM xii (AMNH); Cihuatlán ix (AME); GUA (USNM); LCA vi; MIS i,xii (ADW); PV (Comstock & Vázquez 1961); JAL vii (BMNH).

Mysoria affinis (Herr.-Sch. 1869). AHU vi (ADW); Bahía de Banderas xi; Bahía de CHM iii,xi,xii (AMNH); EBC x (Beutelspacher 1982), ix (Opler 1989); Cihuatlán ix (AME). There is a single specimen of *Mysoria barcastus* (Sepp 1855) in the AMNH labeled from Guadaljara. Since this species is not known from anywhere in western Mexico, and since the specimen is apparently South American in origin, this record is not included in our list. Additionally, several South American satyrines examined in the CUIC have similar false "Guadalajara" labels, and are not listed.

Myscelus amystis hages Godm. & Sal. [1893]. BDT i (ADW).

Phocides belus Godm. & Sal. [1893]. EBC iii (Beutelspacher 1982); PV iv,xii (ADW).

Phocides palemon lilea (Reak. [1867]). AJI vi,ix (AMNH); BDH ii–v (López 1989); EBC ix (Opler 1989); GUA iv,v (AMNH), viii (BMNH); PV xii (ADW).
Phanus marshallii Kirby 1880. MIS iv,xii (ADW); PV (De la Maza 1987).
Udranomia kikkawai (Weeks 1906). BDT xii; MIS iv (ADW).
Proteides mercurius mercurius (Fabr. 1787). BDT i,xii; MIS xii (ADW); PV (Comstock & Vázquez 1961).
Epargyreus exadeus cruza Evans 1952. AJI vi–viii (Freeman unpubl.); BDH iv,v (López 1989); EBC ix (Beutelspacher 1982); PV ix (Comstock & Vázquez 1961); "Jalesco" (sic) (Evans 1952). The exact distribution of this species in western Mexico is uncertain. Some reports of this species before the description of *E. windi* may actually represent *windi*. Some *Epargyreus* specimens examined in this study, including an apparently undescribed species, could not confidently be assigned to any species.
Epargyreus windi Freeman 1969. AHU vi (ADW); AJI vi–x [Type locality] (AMNH, Freeman 1969); BOL (BMNH); EBC ix (Opler, pers. comm., 1993); LCA vi (ADW); LCU, 7 mi S (AMNH).
Epargyreus spina Evans 1952. LCU, 7 mi S (AMNH); MIS i (ADW).
Epargyreus sp. LCA vi; MIS xii (ADW).
Polygonus leo arizonensis (Skinner 1911). BDN iv,xi; BHC (AMNH); MIS i (ADW).
Polygonus manueli Bell & Comstock 1948. BDT i,xii (ADW); EBC ix (Opler, pers. comm., 1993); CHIS xii; MIS i,xii (ADW); JAL vii (BMNH).
Chioides zilpa (Butl. [1872]). AHU vi (ADW); AJI iv,x (AMNH); BDH i,xi,xii (López 1989); BDT i,xii (ADW); EBC ii,ix,x (Beutelspacher 1982), ix (Opler 1989); LCA vi (ADW); LCU vii–viii; LCU, 7 mi S (AMNH); MIS i,iv,xii; PV xii (ADW).
Chioides catillus albofasciatus (Hewit. 1867). AHU vi (ADW); AJI x; Bahía de Banderas xi (AMNH); BDH i,ii,xi,xii (López 1989); BDT i,xii (ADW); CHP v (AMNH); CHIS ii,xii (ADW); BHC (AMNH); GUA vii–x (BMNH); LCA vi (ADW); LCU (AMNH); Lake CHP (BMNH); MAG, 8.7 mi W viii (AME); MIS i–iv,xii; PV i–iv,xii (ADW).
Aguna asander asander (Hewit. 1867). AHU vi (ADW); BDN iv (AMNH); BDT i,xii (ADW); EBC iii (Beutelspacher 1982), ix (Opler 1989); CHIS i,xii; CHI, 2.5 km W, on Hwy 200 xii (ADW); GUA viii (CUIC); LCA vi; MIS i,iv,xii; PV ii (ADW); TEN iv (AMNH); JAL vii (BMNH).
Aguna metophis (Latr. [1824]). BDT i,xii; CHIS xii; MIS i,xii (ADW); PV (Comstock & Vázquez 1961); YEL xii (ADW).
Typhedanus undulatus (Hewit. 1867). BDN iv (AMNH); MIS i (ADW); PV (Comstock & Vázquez 1961).
Typhedanus ampyx (Godm. & Sal. [1893]). BDH xi (López 1989); EBC ix (Beutelspacher 1982); LCA vi; MIS xii (ADW).
Polythrix octomaculata (Sepp 1848). AHU vi; BDT i,xii; MIS i (ADW).
Polythrix asine (Hewit. 1867). AJI x (Freeman unpubl.); BDH v-viii (López 1989); BDT i,xii (ADW); Bahía de CHM iii,xi (AMNH); EBC i,xii (Beutelspacher 1982), ix (Opler 1989); CHIS i,xii (ADW); LCA, 10 mi S LCU vii–viii (AMNH); MIS i,xii (ADW); PV (Comstock & Vázquez 1961); TEN iv (AMNH).
Polythrix mexicanus Freeman 1969. AJI x [allotype female](AMNH, Freeman 1969).
Zestusa staudingeri elwesi (Godm. & Sal. [1893]). AJI v (AMNH).
Codatractus carlos Evans 1952. BDT i,xii; MIS i,xii (ADW).
Codatractus alcaeus alcaeus (Hewit. 1867). BDT i,xii; MIS i,xii (ADW).
Codatractus arizonensis (Skinner 1905). AHU vi (ADW); AJI x (AME), v–ix (AMNH); CHP v; GUA, km 641, Hwy 15 viii (AMNH).
Codatractus sallyae Warren 1995. AHU vi [Type Locality]; LCA vi (Warren 1995a).
Codatractus melon (Godm. & Sal. [1893]). BDH iii (López 1989); EBC v–xii (Beutelspacher 1982), ix (Opler 1989); BHC (AMNH); LCA vi (ADW); PV (Comstock & Vázquez 1961); ZEN vi (ADW); JAL (Evans 1952).
Codatractus bryaxis (Hewit. 1867). LCA vi (ADW).
"Codatractus" hyster (Dyar 1916). AHU vi; LCA vi (ADW).
Urbanus proteus proteus (L. [1758]). AJI v–x (AMNH); BDH xi–xii (López 1989); BDT i,xii; CHIS i,xii (ADW); BHC (AMNH); GUA (BMNH); Hwy 200, 1 km E km 175.5

xii (ADW); Lake CHP (BMNH); MAG, 8.7 mi W viii (AME); MIS i,iii,iv,xii (ADW); PV (Comstock & Vázquez 1961).

Urbanus viterboana (Ehrm. [1907]). AJI ix,xi (AMNH); MIS i (ADW).

Urbanus belli (Hayward 1935). BDT i,xii; CHIS xii; MIS i,xii (ADW).

Urbanus esmeraldus (Butl. 1877). CHIS xii; MIS xii (ADW).

Urbanus evona Evans 1952. CHIS i,xii; MIS xii (ADW).

Urbanus prodicus Bell 1956. MIS xii (ADW).

Urbanus esta Evans 1952. CHIS xii; MIS i,xii (ADW).

Urbanus teleus (Hübner 1821). AHU vi (ADW); BDH v (López 1989); BDT i,xii (ADW); EBC x,xii (Beutelspacher 1982); CHIS xii (ADW); LCA, 10 mi S LCU vii–viii (AMNH); MIS i,xii; PV iv (ADW), ix (AME).

Urbanus procne (Plötz 1881). AHU vi (ADW); AJI v; BDN iv (AMNH); BDT i,xii; CHIS ii,xii (ADW); BHC (AMNH); MAG, 8.7 mi W viii (AME); MIS i,iii,iv,xii; PV iv (ADW); JAL vii (BMNH).

Urbanus simplicius (Stoll 1790). BDN iii (AMNH); BDH i,xii (López 1989); BDT i,xii; CHIS xii (ADW); EBC x (Beutelspacher 1982); MIS i,iii,iv,xii (ADW); PV ii,iv,xii (ADW); Zapotillo (RES).

Urbanus dorantes dorantes (Stoll 1790). AHU vi (ADW); AJI ix; Bahía de Banderas iii,xi; BDN iv,xi (AMNH); BDH i,vii–xi (López 1989); BDT i,xii (ADW); Bahía de CHM xii (AMNH); EBC x (Beutelspacher 1982), ix (Opler 1989); CHIS i,xii (ADW); BHC (AMNH); GUA vii,ix,x (BMNH); LCA vi (ADW); LCA, 10 mi S LCU vii–viii; LCU i; LCU, 7 mi S (AMNH); LDC (Godm. & Sal. 1887–1901); MAG, 8.7 mi W viii (AME); Mirador vii–viii (AMNH); MIS i–iv,xii (ADW); Peñas xi (AMNH); PV i–iv,vi,viii,xii (many); Río San Pedro vii–viii; TEN iv,xi (AMNH); YEL xii; ZEN vi (ADW).

Urbanus chales (Godm. & Sal. [1893]). BDT i,xii; MIS i,xii; PV (ADW).

Astraptes fulgerator azul (Reak. [1867]). AHU vi (ADW); AJI ix (AMNH); BDT i,xii (ADW); Bahía de CHM xii (AMNH); EBC x,xii (Beutelspacher 1982), ix (Opler 1989); CHIS xii (ADW); MIS i,iii,iv,xii; PV ix,xii; YEL xii (ADW).

Astraptes alector hopfferi (Plötz 1882). BDN xi (AMNH); BDH i,xi,xii (López 1989); BDT i,xii (ADW); EBC iii (Beutelspacher 1982), ix (Opler, pers. comm., 1993); CHIS xii; LCA vi (ADW); GUA x (BMNH); MIS i,xii (ADW); TEN ix (AMNH); YEL xii (ADW).

Astraptes anaphus annetta Evans 1952. AHU vi (ADW); Bahía de Banderas xi; BDN xi (AMNH); BDT i,xii (ADW); EBC xii (Beutelspacher 1982), ix (Opler 1989); CHIS xii; MIS i,iii,iv,xii; PV xii (ADW); TEN iv,xi (AMNH); YEL xii (ADW); JAL vii (BMNH).

Astraptes egregius (Butl. 1870). LCA vi (ADW).

Narcosius parisi helen (Evans 1952). BDT i; CHIS xii; MIS xii (ADW); TEN iv (AMNH).

Autochton cellus (Boisd. & LeC. [1837]). AJI vi,vi,ix (AMNH); Atenquique, 13 mi W, 7800' vii (LACM); BDH vii (López 1989); GUA (USNM), ix,x (BMNH); Sayula, 2 mi SW vii–viii (AMNH).

Autochton pseudocellus (Coolidge & Clemence [1910]). Sayula, 2 mi SW vii,viii; Villa Corona, 1 mi E vii–viii (AMNH).

Autochton cinctus (Plötz 1882). GUA iv (AMNH); PLM vi (ADW); Sayula, 2 mi SW vii–viii (AMNH).

Autochton neis (Geyer [1832]). BDT i,xii (ADW); EBC ix,x (Beutelspacher 1982); CHIS xii; LCA vi; MIS i,xii (ADW).

Achalarus casica (Herr.-Sch. 1869). AJI v,ix (AMNH); GUA x (BMNH); GUA, 21 mi N viii (AMNH); MAG, 8.7 mi W viii (AME).

Achalarus toxeus (Plötz 1882). AJI iv–ix (AMNH); Ameca viii (AME); Valle de Autlán vii–viii (AMNH); BDT i,xii (ADW); Bahía de CHM iii, xii (AMNH); GUA (BMNH); LCU, 7 mi S (AMNH); MIS i,xii; PV iv (ADW); JAL (Evans 1955).

Achalarus albociliatus (Mab. 1877). Atenquique v (AME); BDN iv (AMNH); BDH ii–xi (López 1989); PV (Comstock & Vázquez 1961); JAL vii (BMNH).

Thessia jalapus (Plötz 1882). GUA (BMNH).

{***Thorybes drusius*** (Edw. [1884])}. EBC x,xii (Beutelspacher 1982). This locality seems very unlikely for *T. drusius.* Since several skipper species illustrated by Beutelspacher in 1982 were misdetermined, this record may also be in error (it probably represents an *Achalarus*), and until other specimens from Jalisco are examined, this species' ocurrence in Jalisco is listed as hypothetical, although it almost certainly ocurrs in Jalisco at higher elevations to the north around Bolaños.

Thorybes mexicana mexicana (Herr.-Sch. 1869). GUA viii–x (BMNH); Sayula, 2 mi SW vii–vii (AMNH).

"Thorybes" uvydixa Dyar 1914. ZEN vi (ADW).

Cabares potrillo (Lucas 1857). BDT i,xii; CHIS i,xii (ADW); Cihuatlán ix (AME); LCA vi (ADW); LCA, 10 mi S LCU vii-viii (AMNH); MAG, 8.7 mi W viii (AME); MIS i,ii,xii; PV xii (ADW).

Ocyba calathana calanus (Godm. & Sal. [1894]). BDT xii (ADW).

Celaenorrhinus stola Evans 1952. BDT xii; LCA vi; MIS xii; PV xii (ADW).

Celaenorrhinus fritzgaertneri (Bailey 1880). BDH viii–xi (López 1989); MIS xii; ZEN vi (ADW).

Spathilepia clonius (Cr. [1775]). AHU vi; BDT i,xii (ADW); EBC xii (Beutelspacher 1982); MIS i,iv,xii (ADW); PV (Comstock & Vázquez 1961); YEL xii (ADW); JAL vii (BMNH).

Cogia hippalus hippalus (Edw. 1882). EBC ix (Opler 1989); LCA, 10 mi S LCU vii–viii (AMNH); ZEN vi (ADW).

Cogia calchas (Herr.-Sch. 1869). AHU vi (ADW); AJI vi (Freeman unpubl.); BDT i,xii (ADW); La Huerta, 7 mi E (AMNH); MAG, 8.7 mi W viii (AME); MIS i,xii; ZEN vi (ADW); JAL vii (BMNH).

Cogia eluina Godm. & Sal. [1894]. BDH vii (López 1989).

Telemiades choricus (Schaus 1902). MIS xii (ADW).

Telemiades fides Bell 1949. BDT i; CHIS xii; MIS i,xii (ADW).

Arteurotia tractipennis Butl. & Druce 1872. EBC xii (Beutelspacher 1982); ix (Opler 1989).

Polyctor cleta Evans 1953. BDT i,xii (ADW); EBC ix (Opler 1989); CHIS xii; LCA vi; MIS i,xii (ADW); JAL vii (BMNH).

Nisoniades rubescens (Möschler 1876). BDT i,xii; MIS i,xii; PV i,xii (ADW).

Nisoniades ephora Herr.-Sch. 1870. AHU vi (ADW); AJI xi (AMNH).

Pellicia arina Evans 1953. MIS i,xii; PV xii (ADW).

Pellicia dimidiata dimidiata Herr.-Sch. 1870. AHU vi; BDT xii; LCA vi; MIS i (ADW).

Noctuana stator (Godm. & Sal. [1899]). AJI vii (Freeman unpubl.).

Noctuana noctua bipuncta (Plötz 1884). PLM vi (ADW).

Bolla subapicatus (Schaus 1902). AJI viii–x (AMNH); GUA ix (BMNH); LCA vi (ADW).

Bolla orsines (Godm. & Sal. [1896]). AJI v–x (AMNH); LCA vi (ADW); LCU i (AMNH); LDC [Type Locality] (Godm. & Sal. 1887–1901, BMNH); MIS xii (ADW).

Bolla eusebius (Plötz 1884). LCA ix, MIS xii; PLM vi (ADW).

Bolla evippe (Godm. & Sal. [1896]). AHU vi (ADW).

Bolla clytius (Godm. & Sal. [1897]). AJI viii–x (Freeman unpubl.); EBC x (Beutelspacher 1982).

Bolla litus (Dyar 1912). AJI vii–x; Autlán Valley vii–viii; GUA, km 641, Hwy 15 viii (AMNH); MAG, 8.7 mi W viii (AME).

Staphylus tierra Evans 1953. AHU vi (ADW); AJI vii (AMNH); BDT xii (ADW); EBC xii (Beutelspacher 1982); CHIS xii (ADW); GUA v (AMNH); LCA vi (ADW); LCA, 10 mi S LCU vii–VIII(AMNH); MAG, 8.7 mi W viii (AME); MIS i,ii,iv,xii; PV iii,xii (ADW); JAL vii (BMNH).

Staphylus azteca (Scudder 1872). BDT xii (ADW); GUA ix; Lake CHP (BMNH); MIS i,xii; PV xii (ADW).

Staphylus vincula (Plötz 1886). AJI viii–x (AMNH); Lake CHP (BMNH); Río San Pedro vii–viii (AMNH).

Staphylus iguala (Williams & Bell 1940). LCA vi (ADW); LCA, 10 mi S LCU vii–viii (AMNH); PLM vi; ZEN vi (ADW).

Staphylus vulgata (Möschler 1878). LCA vi (ADW).

Gorgythion begga pyralina (Möschler 1876). AHU vi; BDT xii (ADW); EBC ii (Beutelspacher 1982); CHIS xii; MIS i,ii,xii; PV xii; ZEN vi (ADW).
Zera hyacinthinus (Mab. 1877). AJI ix,x (Freeman 1966, AMNH); BDT xii; MIS xii (ADW); PV vi (AME).
Quadrus cerialis (Stoll [1782]). BDT i,xii (ADW); GUA (AME); MIS xii (ADW).
Quadrus lugubris (Feld. [1869]). BDT i,xii; CHIS xii; LCA vi; MIS i,xii (ADW).
Sostrata bifasciata nordica Evans 1953. MIS xii (ADW); TEN iv (AMNH).
Paches polla (Mab. 1888). BDT xii; CHIS xii; MIS i,xii (ADW).
Atarnes sallei (Feld. & Feld. [1867]). BDT xii (ADW); EBC i (Beutelspacher 1982); CHIS i,xii; MIS i,xii (ADW).
Carrhenes canescens canescens (Feld. 1869). EBC ix (Beutelspacher 1982); CHIS xii (ADW); LCA, 10 mi S LCU vii–viii (AMNH); MIS i,xii (ADW); JAL vii (BMNH).
Carrhenes fuscescens (Mab. 1891). EBC ix (Opler, pers. comm., 1993); LCA vi (ADW); PV (Comstock & Vázquez 1961).
Mylon lassia (Hewit. [1868]). JAL (Freeman unpubl.).
Mylon menippus (Fabr. 1777). BDT i,xii; CHI, 2.5 km W, on Hwy 200 i; MIS i,iii,iv,xii (ADW).
Mylon pelopidas (Fabr. 1793). Bahía de Banderas xi (AMNH); LCA vi; MIS i (ADW); PV (Comstock & Vázquez 1961); TEN iii, xi (AMNH); JAL vii (BMNH).
Xenophanes tryxus (Stoll [1780]). CHIS i; MIS i,xii; PV xii (ADW).
Clito clito (Fabr. 1787). BDT xii; MIS iv (ADW).
Antigonus nearchus (Latr. [1813]). BDT i,xii; MIS i,ii,iv,xii; PV xii (ADW).
Antigonus erosus (Hübner [1812]). AHU vi; BDT i,xii (ADW); EBC ix (Beutelspacher 1982); CHIS i; LCA vi; MIS i,iv,xii; PV i,xii (ADW), ix,x (AME); YEL xii (ADW).
Antigonus emorsa (Feld. 1869). AHU vi (ADW); BDH viii–xi (López 1989); GUA x (BMNH); MAG, 8.7 mi W viii (AME); ZEN vi (ADW).
Antigonus funebris (Feld. 1869). AJI ix,x (AMNH); BDH iv–viii (López 1989); EBC x (Beutelspacher 1982); ix (Opler, Pers. Comm., 1993); BHC (AMNH); LCA vi (ADW); PV (Comstock & Vázquez 1961).
Systasea pulverulenta (Feld. 1869). AHU vi (ADW); AJI v (AMNH); LCA vi (ADW); LCA, 10 mi S LCU vii–viii (AMNH); YEL xii (ADW).
Zopyrion sandace Godm. & Sal. [1896]. AHU vi (ADW); BDH v–vii (López 1989); BDT xii (ADW); EBC vii,x (Beutelspacher 1982); ix (Opler 1989); LCA vi; MIS xii; PV xii (ADW); TEN xi (AMNH); ZEN vi (ADW).
Achlyodes busirus heros Ehrm. 1909. BDT xii; CHIS i,xii; MIS iv,xii (ADW); PV (Comstock & Vázquez 1961); YEL xii (ADW); JAL vii (BMNH).
Achlyodes selva Evans 1953. AJI iv,v (AMNH); BDH i–v (López 1989).
Eantis tamenund (Edw. [1871]). AHU vi; BDT xii (ADW); EBC x (Beutelspacher 1982); CHIS xii (ADW); LCA, 10 mi S LCU vii–viii (AMNH); MIS i,xii (ADW).
Grais stigmaticus stigmaticus (Mab. 1883). MIS xii (ADW); PV (Comstock & Vázquez 1961).
Doberes hewitius (Reak. [1867]). JAL vii (AMNH).
Timochares trifasciata trifasciata (Hewit. 1868). BDT i,xii (ADW); EBC i,xii (Beutelspacher 1982); CHIS xii (ADW); BHC (AMNH); MIS i,iv,xii (ADW); PV (Comstock & Vázquez 1961).
Timochares ruptifasciata ruptifasciata (Plötz 1884). LCU vii–viii (AMNH); PV (Comstock & Vázquez 1961); JAL (BMNH).
Anastrus sempiturnus sempiturnus (Butl. & Druce 1872). AHU vi (ADW); AJI ix (AMNH); BDT i; CHI, 2.5 km W, on Hwy 200 i; MIS i,xii; PV i,iii,xii; (ADW).
Anastrus robigus (Plötz 1884). MIS i,iv,xii (ADW); PV (Comstock & Vázquez 1961).
Cycloglypha thrasibulus thrasibulus (Fabr. 1793). BDT i,xii; CHIS xii; MIS i,xii (ADW); PV (De la Maza 1987); iii,xii (ADW); JAL vii (BMNH).
Ebrietas anacreon anacreon (Staud. 1876). BDH i (López 1989); BDT xii (ADW); EBC x (Beutelspacher 1982); MIS xii (ADW).
Theagenes albiplaga aegides (Herr.-Sch. 1869). LCU vii–viii (AMNH).
Chiomara mithrax (Möschler 1878). BDH viii (López 1989); EBC vii (Beutelspacher 1982); CHIS i; LCA vi (ADW); PV (Comstock & Vázquez 1961).

Chiomara asychis georgina (Reak. 1868). AJI ix (AMNH); BDH xi,xii (López 1989); EBC ii (Beutelspacher 1982); ix (Opler 1989); GUA ix (BMNH); PV (Comstock & Vázquez 1961).

Gesta gesta invisus (Butl. & Druce 1872). AJI viii; Bahía de Banderas iii (AMNH); BDT i,xii (ADW); EBC x (Beutelspacher 1982); CHIS i,xii (ADW); GUA ix (BMNH); LCU vii–viii (AMNH); MIS i,xii; PV i,iv,viii,xii (ADW).

Erynnis funeralis (Scudder & Burgess 1870). AHU vi (ADW); AJI viii (AMNH); Ameca viii (AME); Valle de Autlán vii–viii (AMNH); CHIS xii (ADW); LDC (Godm. & Sal. 1887–1901); MAG, 8.7 mi W viii (AME).

Erynnis scudderi (Skinner 1914). BOL (BMNH). See Burns (1964).

Erynnis juvenalis clitus (Edw. 1883). JAL (Evans 1953).

Erynnis tristis tatius (Edw. 1883). LCA vi (ADW); LCU (AMNH).

{***Erynnis mercurius*** (Dyar 1926)}. BDH iv (López 1989) Although the only previously known specimens of *mercurius* are from D.F. (Burns 1964), it is possible that *mercurius* does occur in Jalisco. Until specimens are examined, however, this species is listed as hypothetical for Jalisco.

Pyrgus communis (Grote 1872). AJI; Atenquique vii (Freeman unpubl.); BDH ii–xi (López 1989). We have not examined any genitalically typical *communis* specimens in this study.

Pyrgus albescens Plötz 1884. AHU vi (ADW); AJI; Autlán Valley, vii,viii (Freeman unpubl.); BHC; GUA v (AMNH), ix,x (BMNH); Lake CHP (Evans 1953); Mirador vii–viii (AMNH); PLM vi (ADW); Sayula, 1 mi W vii,viii (AMNH); ZEN vi (ADW). Several specimens from Ahuacupán, and one specimen from Zenzontla have forewing costal folds, typical of *albescens*, but the valvae are not toothed, and are very smooth, as in *Pyrgus adepta* Plötz, 1884. These specimens may be integrades between *albescens* and *adepta*.

Pyrgus oileus oileus (L. 1767). AHU vi (ADW); AJI ix (Freeman unpubl.); Valle de Autlán xi (AMNH); BDT i,xii (ADW); Bahía de CHM xi (AMNH); EBC iii (Beutelspacher 1982); CHP v (AMNH); CHIS i,xii (ADW); BHC (AMNH); LCA vi (ADW); LCA, 10 mi S LCU vii–viii (AMNH); MAG, 8.7 mi W viii (AME); MIS i–iv,xii (ADW); Peñas xi (AMNH); PV i–iv,xii (ADW); TEN (AMNH); ZEN vi (ADW).

Pyrgus philetas Edw. 1881. MAG, 8.7 mi W viii (AME); Sayula, 1 mi SW vii–viii; Villa Corona, 1 mi E vii–viii (AMNH).

Heliopetes domicella domicella (Erichson 1848). AJI ix (AMNH); MAG, 8.7 mi W viii (AME).

Heliopetes macaira macaira (Reak. [1867]). AHU vi (ADW); AJI ix (Freeman unpubl.); BDH vii–xi (López 1989); BDT xii (ADW); EBC iii,vi (Beutelspacher 1982); CHIS xii (ADW); GUA ix (BMNH); LCA vi (ADW); Lake CHP (BMNH); MIS i–iv,xii; PV i,iii,iv,xii; ZEN vi (ADW).

Heliopetes laviana laviana (Hewit. [1868]). AHU vi (ADW); Valle de Autlán vii–viii (AMNH); BDH vii–xi (López 1989); BDT xii (ADW); EBC iii (Beutelspacher 1982), ix (Opler 1989); CHIS xii (ADW); GUA ix (BMNH); LCA, 10 mi S LCU vii–viii (AMNH); MAG, 8.7 mi W viii (AME); MIS xii; PV xii (ADW).

Heliopetes arsalte arsalte (L. 1758). BDH x (López 1989); EBC iii (Beutelspacher 1982); PV i (ADW).

Heliopetes alana (Reak. 1868). BDT xii (ADW); LCA, 10 mi S LCU vii–viii (AMNH); MIS i,iii,iv,xii (ADW); TEN iv (AMNH).

Pholisora mejicana (Reak. [1867]). AJI vii (AMNH); GUA (Evans 1953); LDC (Godm. & Sal. 1887–1901); La Huerta, 1 mi E vii–viii; Villa Corona, 1 mi E vii–viii (AMNH).

Piruna brunnea (Scudder 1872). LCA, 10 mi S LCU vii–viii (AMNH).

Piruna gyrans (Plötz 1884). BOL (Godm. & Sal. 1887–1901). *Piruna sticta* Evans, 1955, also described from Bolaños, is a synonym of *gyrans* (Freeman, pers. comm., 1995).

Piruna microsticta (Godman [1900]). BDH vii (López 1989); JAL (Freeman unpubl.).

Piruna penaea (Dyar 1918). Valle de Autlán vii–viii (AMNH); MAG, 8.7 mi W viii (AME).

Piruna ajijicensis Freeman 1970. AJI vii–xi [Type Locality](Freeman 1970, AMNH).

Piruna sp. nov. AJI ix (AMNH).

Dardarina dardaris (Hewit. 1877). Valle de Autlán vii–viii (AMNH); GUA (AMNH), ix (BMNH); MAG, 8.7 mi W viii; Tizapán, vii (AME).

Dalla faula (Godman [1900]). GUA [Type Locality](Godm. & Sal. 1887–1901, BMNH); LCA, 10 mi S LCU vii-viii (AMNH).

Dalla dividuum (Dyar 1913). LCA vi (ADW).

Dalla ligilla (Hewit. 1877). LCA vi (ADW).

Synapte syraces (Godman [1901]). CHIS i; LCA vi; ZEN vi (ADW).

Synapte shiva Evans 1955. BDH ii–iii,xi–xii (López 1989); BHC (AMNH); GUA (USNM); LCA, 10 mi S LCU vii–viii (AMNH); Lake CHP (BMNH); MAG, 8.7 mi W viii (AME); PV (Comstock & Vázquez 1961). Some of these literature records may refer to *syraces*.

Zariaspes mythecus (Godman [1900]). BDT xii; CHIS xii; MIS i,xii; PV xii (ADW).

Corticea corticea (Plötz 1883). BDT i (ADW); GUA (USNM); MIS i,iii,xii; PV i,iii,iv,xii (ADW).

Callimormus saturnus (Herr.-Sch. 1869). BDT i,xii; CHIS xii; LCA vi (ADW); MAG, 8.7 mi W viii (AME); MIS i,iii,iv,xii (ADW); Plan de Barraneasa, 1 mi W vii (AMNH); PV iii,xii (ADW).

Eprius veleda (Godman [1901]). AJI x (AMNH).

Mnasicles sp. nov. CHIS xii; PLM vi (ADW).

Methionopsis ina (Plötz 1882). BDT xii (ADW); CHP (Freeman unpubl.); CHIS i,xii; MIS i,iv,xii; PV xii (ADW).

Flaccilla aecas (Stoll [1781]). MIS xii (ADW).

Phanes aletes (Geyer [1832]). MIS i,xii (ADW).

Vidius perigenes (Godman [1900]). JAL (Freeman unpubl.).

Monca tyrtaeus (Plötz 1883). MIS i,xii (ADW).

Nastra julia (Freeman 1945). AJI ii (AMNH); MAG, 8.7 mi W viii (AME); Mirador vii–viii (AMNH).

Cymaenes odilia trebius (Mab. 1891). BDT xii; CHIS xii (ADW); GUA (BMNH); MIS i,iv,xii; PV iii,xii (ADW).

Vehilius inca (Scudder 1872). AHU vi (ADW); GUA (USNM); LCA vi; MIS xii; PV iii (ADW).

Vehilius illudens (Mab. 1891). JAL (Freeman unpubl.).

Mnasilus allubitus (Butl. 1877). "San Blas, Jalisco" (BMNH).

Remella remus (Fabr. 1798). BDT i,xii (ADW); EBC ix (Opler, pers. comm., 1993); MIS xii (ADW).

Remella rita (Evans 1955). JAL (AMNH).

Lerema accius accius (Smith 1797). AHU vi (ADW); AJI ix (AMNH); BDT i,xii (ADW); CHP ii (AMNH); GUA viii (AMNH), ix (BMNH); Hwy 200, 1–2 km E, km 175.5 i (ADW); LCA, 10 mi S LCU vii–viii (AMNH); MIS i,xii; PV iii,xii (ADW). More than one species may be represented by these records.

Lerema liris Evans 1955. EBC ix (Beutelspacher 1982); GUA ix (BMNH); GUA, km 641, Hwy 15 viii (AMNH); PV (Comstock & Vázquez 1961).

Morys valda Evans 1955. LCA vi; MIS i,iv,xii (ADW).

{**Tigasis zalates** Godman [1900]}. EBC iii (Beutelspacher 1982). Beutelspacher's illustration of "*zalates*" is apparently a *Lerema* species. Until specimens are examined, this species listing for Jalisco is hypothetical.

Vettius fantasos (Stoll [1780]). BDT xii; CHIS i; LCA vi; MIS i,xii; PV xii (ADW); Tonila x (MZFC); YEL xii (ADW).

Perichares philetes adela (Hewit. [1867]). BDT i (ADW); EBC i (Beutelspacher 1982); MIS i,xii; PV xii (ADW).

Lycas argentea (Hewit. [1866]). LCA vi (ADW).

Quinta cannae (Herr.-Sch. 1869). MIS i,xii; PV xii (ADW).

Rhinthon osca (Plötz 1883). GUA ix–x (BMNH).

Mucia zygia (Plötz 1886). CHIS i; PV iii (ADW).

Conga chydaea (Butl. 1877). BDT i; MIS i,xii (ADW).

Ancyloxypha arene (Edw. [1871]). ADJ, 2 mi S vii–viii; AJI vii,x (AMNH); BDT i,xii

(ADW); EBC ix (Beutelspacher 1982); CHI i (ADW); GUA ix (BMNH); Hwy 200, 4.3 km W km 175.5 i; MIS xii; PV iii,iv (ADW).

Copaeodes minima (Edw. 1870). AJI x (AMNH); BDH i (López 1989); BDT i; CHIS xii (ADW); BHC (AMNH); GUA v (AMNH); LCA vi (ADW); Lake CHP (BMNH); MIS xii; PV iv,xii (ADW); Sayula, 1 mi SW vii–viii; Villa Corona, 1 mi E vii–viii (AMNH).

Copaeodes aurantiaca (Hewit. [1868]). Lake CHP (BMNH).

Adopaeoides prittwitzi (Plötz 1884). JAL (Freeman unpubl.).

Hylephila phyleus phyleus (Drury [1773]). ADJ, 2 mi S vii–viii (AMNH); BDH i–v (López 1989); BDT i,xii (ADW); EBC iii,viii,ix (Beutelspacher 1982); CHIS xii (ADW); BHC (AMNH); El Tuito, N of viii (RES); MIS i,iii,iv,xii; PV i,iii,iv,xii (ADW); Villa Corona, 1 mi E vii–viii (AMNH).

Polites subreticulata (Plötz 1883). CHIS xii (ADW); PV xii (AMNH).

Polites vibex praeceps (Scudder 1872). BDH vii–viii (López 1989); BDT i,xii; CHIS xii; LCA vi (ADW); MAG, 8.7 mi W viii (AME); MIS i,iv,xii (ADW); Peñas xi (AMNH); PV i,ii,xii (ADW).

Polites puxillius (Mab. 1891). BOL (Godm. & Sal. 1887–1901). See Burns (1994a).

Polites pupillus (Plötz 1883). BOL (Evans 1955, BMNH).

Pseudocopaeodes eunus chromis (Skinner 1919). GUA ix (BMNH).

Wallengrenia otho otho (Smith 1797). BDT i,xii; CHIS xii; MIS i,xii (ADW).

Pompeius pompeius (Latr. [1824]). AHU vi; BDT i,xii; CHIS xii; MIS i,iv,xii; PV i,iii,xii (ADW).

Anatrytone mazai (Freeman 1969). El Tuito, N of viii (RES). See Burns (1994b).

Paratrytone sp. BDH iii–v (López 1989); GUA, km 641, Hwy 15 viii (AMNH). Up to four species of *Paratrytone* may occur in Jalisco at high elevations.

Ochlodes samenta Dyar 1914. JAL (Freeman unpubl.).

Poanes zabulon (Boisd. & LeC. [1837]). CHP v (AMNH).

Poanes taxiles (Edw. 1881). BOL (BMNH). See Burns (1992b).

Poanes melane vitellina (Herr.-Sch. 1869). AJI iv,v (AMNH); BDH vii (López 1989); GUA ix (BMNH).

Poanes inimica (Butl. & Druce 1872). BDH viii (López 1989).

"*Poanes*" *benito* Freeman 1979. LCA, 10 mi S LCU vii,viii [Type Locality](Freeman 1979, AMNH). See Burns (1992b).

Quasimellana aurora (Bell 1942). Hwy 200 nr Vallarta, Las Juntas-Verano 1000′ viii (USNM); LCA vi; PLM vi (ADW). See Burns (1994b).

Quasimellana balsa (Bell 1942). BDT xii; LCA vi (ADW); Tomatlán, 13 mi N (Burns, pers. comm., 1995).

Quasimellana eulogius agnesae (Bell 1959). PV xii (ADW).

Quasimellana mulleri (Bell 1942). LCU, 7 mi S 3200' (AMNH). See Burns (1994b).

Halotus rica (Bell 1942). GUA (USNM).

Halotus jonaveriorum Burns 1992. LCU, 7 mi S (AMNH).

Metron chrysogastra (Butl. 1870). CHIS i (ADW).

Atrytonopsis edwardsi B. & McD. 1916. AJI ix (AMNH); BDH i–iii,xi–xii (López 1989); GUA (Burns 1983).

Amblyscirtes folia Godman [1900]. AHU vi (ADW); AJI viii–x (AMNH); GUA (USNM); LCA vi (ADW); LCA, 10 mi S LCU vii–viii; LCU (AMNH); Lake CHP (BMNH), ix–x (Freeman 1973).

Amblyscirtes exoteria (Herr.-Sch. 1869). BOL (BMNH).

Amblyscirtes cassus Edw. 1883. AJI x (AMNH).

Amblyscirtes fluonia Godman [1900]. AJI vii–ix (AMNH); GUA (USNM), ix (BMNH); Lake CHP (BMNH); MAG, 8.7 mi W viii (AME).

Amblyscirtes tolteca tolteca Scudder 1872. AHU vi (ADW); BDH vi (López 1989); GUA ix (BMNH); LCA vi (ADW); MAG, 8.7 mi W viii (AME); PV (Comstock & Vázquez 1961); ZEN vi (ADW).

Amblyscirtes elissa arizonae Freeman 1993. CHP vi (Freeman 1993).

"*Amblyscirtes*" *florus* (Godman [1900]) (=*Repens repta* Evans 1955). AJI ix (Freeman unpubl.); GUA ix [*repta* Type Locality](Evans 1955, BMNH); LCU vii,viii (AMNH).

Lerodea eufala (Edw. 1869). Bahía de Banderas iii (AMNH).
Lerodea dysaules Godman [1900]. AJI vii,ix (AMNH); MIS i,xii; PV i,xii (ADW).
Calpodes ethlius (Stoll [1782]). GUA ix (BMNH); MIS i,xii (ADW).
Panoquina errans (Skinner 1892). Bahía de CHM xi; Bahía de TEN xi (AMNH).
Panoquina ocola (Edw. 1863). BDT i,xii (ADW); EBC i (Beutelspacher 1982); CHIS i; CHI, 2.5 km W, on Hwy 200 i; LCA vi; MIS i,iv,xii; PV i–iii,xii (ADW).
Panoquina hecebola (Scudder 1872). MAG, 8.7 mi W viii (AME).
Panoquina sylvicola (Herr.-Sch. 1865). BDT i; CHI, on Hwy 200 i; LCA vi; MIS i (ADW).
Panoquina evansi (Freeman 1946). CHI, on Hwy 200 i; CHI, 2.5 km W, on Hwy. 200 i; MIS xii; PV xii (ADW).
Zenis jebus janka Evans 1955. BDT i; CHIS i; CHI, 2.5 km W, on Hwy 200 i; LCA vi; MIS xii (ADW).
Nyctelius nyctelius nyctelius (Latr. [1824]). AJI ix (AMNH); BDT i; CHIS xii (ADW); BHC (AMNH); GUA ix (BMNH); MIS i,xii (ADW).
Thespieus macareus (Herr.-Sch. 1869). AJI v,ix (AMNH) BDH iii (López 1989); GUA v (AMNH).
Thespieus dalman guerreronis Dyar 1913. BDT xii; CHIS xii (ADW).
Vacerra aeas (Plötz 1882). MIS i,xii (ADW).
Vacerra gayra (Dyar 1918). BDT xii; MIS i,xii (ADW).
Vacerra lachares Godman [1900]. MIS i (ADW). Steinhauser's (1974) figure of the genitalia of *V. lachares* is actually *V. gayra*. Our useage of the name *lachares* here is tentative, because the type of *lachares* is a female from Costa Rica, and the only similar Mexican specimens that have been examined (from Nayarit and Jalisco) are males.
Vacerra cervara Steinhauser 1974. MIS xii (ADW). This is the first record of this species from México.
Niconiades xanthaphes Hübner [1821]. MIS xii (ADW).
Aides dysoni Godman [1900]. MIS i,xii (ADW); Peñas xi (AMNH); PV (Comstock & Vázquez 1961).
Saliana esperi Evans 1955. MIS xii (ADW).
Saliana fusta Evans 1955. LCA vi; MIS i,xii (ADW).
Saliana longirostris (Sepp 1848). BDT xii; LCA vi; MIS i,xii (ADW).
Thracides phidon (Cr. [1779]). MIS xii (ADW).
Neoxeniades luda (Hewit. 1877). MIS i,xii (ADW).
Stallingsia smithi (Druce 1896). GUA, km 641, Hwy 15 vi (AMNH).
Aegiale hesperiaris (Walker 1856). Quila (De la Maza 1987).
Agathymus fieldi Freeman 1960. GUA, km 724, Hwy 15 ix (AME); x (AMNH).
Agathymus rethon (Dyar 1913). AHU vi (ADW).

PAPILIONIDAE (28 SPECIES)

Baronia brevicornis brevicornis Salvin 1893. Río Ayuquilla (Beutelspacher 1984); ZEN vi,vii (MZFC).
Battus philenor philenor (L. 1771). ADJ (Rodríguez 1982), vi (CIB); Amatitlán (Beutelspacher 1984); BDH iii–v (López 1989); BES ii–v,vii–xi (IMCyP, Abud 1987,1988); CHP (AMNH); GUA (AME, De la Maza 1987); Sayula; TEN (AMNH); Tequila (Beutelspacher 1984).
Battus polydamas polydamas (L. 1758). AHU iii,vi,x (MZFC); Autlán (Beutelspacher 1984); Bahía de Banderas; BDN (AMNH); BDH v–viii (López 1989); BDT i,xii (ADW); CHM (AMNH); EBC vii,x (UCB); iii,viii–xii (Beutelspacher 1982), ix (Opler 1989); CHIS xii (ADW); BHC (AMNH); Hotel El Dorado, on Hwy 200 iv (LACM); LCA vi (ADW); Melaque, 5 km N xii (UCB); MIS i–iv,xii (ADW); MIS, 12 km S PV iv (LACM); PV (De la Maza 1987), ii,iv,vi,ix,x,xii (LACM), xi,xii (CAS), i,iii,iv,xii (ADW); RT at Hwy 200 i (LACM); TEN (AMNH), i,iii (LACM); YEL ii–iv,viii (LACM), xii (ADW).
Battus laodamas iopas (Godm. & Sal. 1897). EBC viii (Beutelspacher 1982); LCA

ix,v,vi,x,xi (MZFC); LCA, 10 mi S LCU (AMNH); Melaque Jct, 17 km NNE x (UCB); MIS (De la Maza 1987); PV (De la Maza 1987), ix (LACM), iv (ADW), viii, ix (Comstock & Vázquez 1961, Tyler et. al. 1994); TEN xi (AMNH); Tequila (Beutelspacher 1984); ZEN vi (ADW).

Battus eracon (Godm. & Sal. 1897). Autlán (Beutelspacher 1984, CIB); BDN xi (AMNH); BDH xi,xii (López 1989); EBC vii (UCB), ii,iii,vi,viii,x (Beutelspacher 1982); Cihuatlán xii (AME); Melaque, 8 km N xii (UCB); MIS xii (ADW); PLM xii (CAS); PV (De la Maza 1987), xii (CAS), iv (ADW); TEN xi (AMNH).

Parides alopius (Godm. & Sal. 1890). AJI (De la Maza 1987); BDH x–xii (López 1989); BES i,iii,v,vi,viii,ix,x (IMCyP, Abud 1987,1988); CHP v (AMNH); GUA (many), v (AME), viii,x (Rothschild & Jordan 1906); Tepatitlán (Tyler 1975, Beutelspacher 1984); Tequila (Beutelspacher 1984).

Parides photinus photinus (Doubleday 1844). AHU ii,iii,v,vi,viii; ECAL iii (MZFC); Bahía de Tenacatita i,iii (LACM); BDN xii (AMNH); BDH ii–iv,x,xi (López 1989); BDT xii (ADW); BES ii–vi,ix,x (IMCyP, Abud 1987,1988); CHM xi (AMNH); EBC x,xii (Beutelspacher 1982); CHP v,x (LACM); CHIS i,xii (ADW); LCA i,ii,vi,vii,ix,x; ECLO iii (MZFC); Melaque, 5 km N xii; Melaque, 8 km N x,xii (UCB); MIS i,iv,xii (ADW); ECPE iii; PLM i,ii,vi,ix–xi (MZFC); PV (Comstock & Vázquez 1961), xi,xii (CAS), iii,iv,xii (ADW); RT, at Hwy 200 i (LACM); TEN x,xi (AMNH); Tequila xii (many); YEL xii (ADW), xi (CAS); ZEN viii (MZFC).

Parides montezuma montezuma (Westw. 1842). ADJ (Rodríguez 1982), vi–xi (CIB); Autlán (Beutelspacher 1984); AHU iii,iv,vi,viii,x,xi (MZFC); BDN, nr. xii (LACM); BDH v–viii (López 1989); BDT xii (ADW); CHM (Rodríguez 1982); EBC ix (CAS), iii, viii–xii (Beutelspacher 1982), ix (Opler 1989); CHP v (AMNH), x (LACM); CHIS i,xii (ADW); El Tuito (De la Maza 1987); GUA (USNM), x (Rothschild & Jordan 1906); LCA ii,viii–xi (MZFC); MIS i,iii,iv,xii (ADW); MIS, 12 km S PV iv (LACM); PV (Comstock & Vázquez 1961, Tyler 1975), ii,viii,x,xi (CAS), iii (ADW); Tecalitlán, 6 km S ix (CAS); TEN xi (AMNH); Tepic viii (CAS); Tomatlán-El Tuito (Beutelspacher 1984); YEL xii (ADW); ZEN vi (MZFC).

Parides erithalion trichopus (Rothschild & Jordan 1906). AHU v,vi,x,xi (MZFC); BDH iii,iv,viii,x (López 1989); EBC vii (UCB); CHIS i (ADW); El Tuito (Beutelspacher 1984); Hwy 200, 1 km W km 175.7 i (ADW); LCA ii,viii (MZFC); La Resolana, 25 mi SW xi (AMNH); PLM vi,viii (MZFC); PV ix (De la Maza 1980); RT at Hwy 200 i (LACM); ZEN viii (MZFC).

Protographium epidaus tepicus (Rothschild & Jordan 1906). ADJ (Rodríguez 1982), viii (CIB); AHU v,vi (MZFC); BDH iv,vi (López 1989); CHM (Rodríguez 1982), viii (UCB); EBC viii (Beutelspacher 1982); GUA (many); GUA, 2 mi S vi (UCB); LCA v,vi (MZFC); MIS iv (ADW); PV (De la Maza 1987, Comstock & Vázquez 1961), vii,viii (AME), vii,viii,x (LACM), iv (ADW); YEL viii (LACM); ZEN vi (MZFC).

Protographium philolaus philolaus (Boisd. 1836). EBC vii (UCB); vii,viii (Beutelspacher 1982); BHC (AMNH); LCA vi (ADW); PV (Comstock & Vázquez 1961) vii (LACM), xii (CAS).

{***Protographium calliste calliste*** (Bates 1864)}. JAL (Rothschild & Jordan 1906).

Protographium agesilaus fortis (Rothschild & Jordan 1906). JAL (Tyler et al. 1994).

Mimoides thymbraeus aconophos (Gray [1853]). ADJ (Rodríguez 1982), viii (CIB); AHU vi (ADW), x (MZFC); BDH i,v (López 1989); BES vi,x (IMCyP, Abud 1987,1988); El Tuito (De la Maza 1987); GUA (AMNH, USNM), x (Rothschild & Jordan 1906); LCA vi (ADW); LCU ix (AMNH); PV (Comstock & Vázquez 1961); Tamazula vii (CAS); Tomatlán-El Tuito (Beutelspacher 1984); ZEN vi (ADW).

Mimoides ilus occiduus (Vázquez 1957). Autlán vii (CAS); EBC vi (Beutelspacher 1982); PV VII; Tamazula vii (CAS).

Priamides pharnaces (Doubleday 1846). ADJ (Rodríguez 1982),vi–xi (CIB); AHU vi (MZFC); Autlán (Beutelspacher 1984); BDH v–ix (López 1989); BDT i,xii (ADW); CHM (Rodríguez 1982); EBC x (Beutelspacher 1982); CHP x (LACM); CHIS xii (ADW); GUA (USNM), v (LACM), vii–x (Rothschild & Jordan 1906); MIS i,xii (ADW); Ocotlán ix (USNM); PV iv (ADW).

Priamides erostratus vazquezae (Beutelspacher 1976). AHU ix (MZFC); Tapalapa vii (AME); ZEN xi (MZFC)

Priamides anchisiades idaeus (Fabr. 1793). BDH vi,vii (López 1989); EBC xii (Beutelspacher 1982); MIS xii; PV iv (ADW).

Troilides torquatus mazai (Beutelspacher 1976). MIS ix,x [Type Locality](Beutelspacher 1976b, CIB, Vázquez & Zaragoza 1979); PV (Beutelspacher 1984, De la Maza 1987), ix,x (Beutelspacher 1974).

Calaides ornythion ssp. EBC vii,viii (Beutelspacher 1982); PV (Comstock & Vázquez 1961).

Calaides astyalus bajaensis (Brown & Faulkner 1992). EBC vii (UCB); PV (Comstock & Vázquez 1961).

Calaides androgeus ssp. EBC viii (Beutelspacher 1982); LCA vi,xi; PLM xi (MZFC); PV (Comstock & Vázquez 1961); Tonila x (SDNHM).

Heraclides thoas autocles (Rothschild & Jordan 1906). AHU iii (MZFC); BDT xii (ADW); EBC vii,xi (UCB), viii (Beutelspacher 1982), ix (Opler, pers. comm., 1993); LCA viii,ix,x (MZFC); Melaque, 5 km N xii; Melaque, 8 km N xii (UCB); MIS i,iii,xii (ADW); MIS, 12 km S PV iv (LACM); PLM viii (MZFC); PV viii,x (LACM), iii,xii (ADW), ix (Comstock & Vázquez 1961); TEN (AMNH); YEL iv,viii (LACM), xii (ADW); ZEN viii (MZFC).

Heraclides cresphontes (Cr. 1777). ADJ (Rodríguez 1982), vi-viii,x,xi (CIB); AHU iii,v,vi,xi (MZFC); BDH iv,viii,xii (López 1989); BDT i,xii (ADW); CHM (Rodríguez 1982); EBC vii,xi (UCB), ii,vi,xii (Beutelspacher 1982), ix (Opler 1989); CHP (AMNH); CHIS xii (ADW); GUA (AMNH), v (Tyler et. al. 1994), viii (LACM), vii,ix,x (Rothschild & Jordan 1906); Melaque, 8 km N xii (UCB); MIS i,iii,iv,xii (ADW); PLM viii (MZFC); PV ix,x (LACM), iii,xii (ADW); Tecolotlán, 3 km NE vii (CMNH); Valle de Autlán (AMNH); ZEN v (MZFC).

Papilio polyxenes asterius Stoll 1782. ADJ (Rodríguez 1982), iv–viii (CIB); AHU vi,xi (MZFC); BDH x,xii (López 1989); BES ii (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); CHP; LCU (AMNH); GUA (many); LCA xi (MZFC).

Pterourus multicaudatus (Kirby 1884). ADJ (Rodríguez 1982), vi,x,xi (CIB); BDH i–xii (López 1989); CHM (Rodríguez 1982); GUA vii (AMNH), viii (Rothschild & Jordan 1906); Ocotlán x; PV xii (CAS).

Pyrrhosticta garamas garamas (Geyer [1829]). ADJ (Rodríguez 1982), ii,viii–xi (CIB); ECAL iii (MZFC); BDH i–xii (López 1989); BES iii,iv,vi–x (IMCyP, Abud 1987,1988); CHP x (LACM); GUA (many), v (AMNH), vii (CAS); Mazamitla x (SDNHM); ECPE III; PLM v,x (MZFC); Tapalpa iii (AME, Tyler et al. 1994); Tonila vii (SDNHM).

Pyrrhosticta victorinus morelius (Rothschild & Jordan 1906). AHU iii,viii,x (MZFC); PV (Comstock & Vázquez 1961), iv (ADW).

PIERIDAE (43 SPECIES)

Enantia mazai diazi Llorente 1984. AHU iii,xi (MZFC); BDT i,xii; CHI, on Hwy 200 i (ADW); EBC x (Beutelspacher 1982); Jalpa (AMNH); LCA ix (MZFC); LCU (AMNH); MIS xii (ADW); PLM iii,vi,viii,x,xi (MZFC); PV, 21.7 mi S vii (SDNHM). This species has been confused with *Enantia jethys* (Boisd. 1836) (see Beutelspacher 1988), a species that does not occur in Jalisco.

Lieinix nemesis nayaritensis Llorente 1984. El Durazno, 6 mi E iv (SDNHM); LCA vi,viii,xi; PLM viii,x,xi (MZFC).

Dismorphia amphiona lupita Lamas 1979. CHI i; CHIS i,xii (ADW); LCA ix,xi (MZFC); MIS xii (ADW); PV iv (UCB). See Lamas (1979).

Colias eurytheme Boisd. 1852. ADJ (Rodríguez 1982), ii,v,viii,x,xi (CIB); Ameca viii (AME); BDH vi,viii,ix (López 1989); CHM (Rodríguez 1982); EBC viii (Beutelspacher 1982); GUA; Villa Corona, 1 mi E vii (AMNH).

Zerene cesonia cesonia (Stoll 1791). ADJ (Rodríguez 1982), viii–xi (CIB); AHU viii,x,xi (MZFC); Ameca (CIB, Vázquez 1952), vi,viii (AME); BDH viii,ix (López 1989); BES i,vii–x (IMCyP, Abud 1987,1988); LCU, 7 mi S (AMNH); CHM (Rodríguez 1982);

EBC i–xii (Beutelspacher 1982), ix (Opler 1989); CHIS xii (ADW); ECET iii (MZFC); GUA ix (LACM), vii,viii (many); GUA, 10 mi SW viii (SDNHM); LCA i,ii,v,viii–x (MZFC); La Huerta, 7 mi E (AMNH); MIS iv (ADW); PLM ii,xi (MZFC); PV ix (Comstock & Vázquez 1961); RT at Hwy 200 i (LACM); Tizapán viii (AME); ZEN ix (MZFC).

Anteos clorinde nivifera (Frühstorfer 1907). ADJ (Rodríguez 1982), ix (CIB); AHU vi,viii,x,xi (MZFC); Autlán (AMNH); BDH i–iii,vi,viii (López 1989); BDT i,xii (ADW); BES i–vii,ix,x (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC vii,viii (Beutelspacher 1982), ix (Opler 1989); CHIS xii (ADW); LCA vi,ix–xi; ECLC iv; ECLO iii (MZFC); MIS i,iv,xii (ADW), iv (LACM); Peñas (AMNH); PV iii,iv,xii (ADW); PV, 30 km S on Hwy 200 iv (LACM); Río San Pedro (AMNH); RT at Hwy 200 i (LACM); YEL xii (ADW); ZEN vi,ix,xi (MZFC).

Anteos maerula lacordairei (Boisd. 1836). AHU x,xi (MZFC); BDH i–iii (López 1989); BDT i,xii (ADW); BES i,i–vi,ix,x (IMCyP, Abud 1987,1988); CHIS xii (ADW); ECET iii (MZFC); EBC vii (UCB), iii,viii,ix,x (Beutelspacher 1982), ix (Opler 1989); GUA (Vázquez 1951); LCA ii,vi,viii; ECLO iii (MZFC); MIS i,iv,xii (ADW); PLM viii (MZFC); PV viii (Comstock & Vázquez 1961), x (LACM); iii,iv (ADW); RT at Hwy 200 I; TEN xii (LACM).

Phoebis agarithe agarithe (Boisd. 1836). ADJ (Rodríguez 1982), ii–xi (CIB); AHU iii,vi,x,xi (MZFC); Ameca viii (AME); Valle de Autlán (AMNH); BDH v–ix (López 1989); BDT i,xii (ADW); CHM (AMNH); EBC iii,xii (Beutelspacher 1982), ix (Opler 1989); CHP x (LACM); CHIS i,xii (ADW); Cihuatlán vi (AME); LCU (AMNH); Hwy 185, ca. 21 km N Hwy 190 viii (LACM); LCA viii,xi (MZFC); La Floresta, nr. AJI, LDC ix (UCB); La Huerta, 7 mi E (AMNH); Melaque, 8 km N xii (UCB); MIS i–iv,xii (ADW); Ocotlán iii,x (AME); PV ii (LACM), viii (Comstock & Vázquez 1961), xii (CAS), i,iii,iv,xii (ADW); PV, 22 km S, on Hwy 200 iii; PV, 53 km S, on Hwy 200 i; RT at Hwy 200 i (LACM); TEN (AMNH); YEL xii (ADW); ZEN viii (MZFC).

Phoebis argante argante (Fabr. 1775). AHU v,vi,viii,xi (MZFC); BDN, nr. xii (LACM); BDT i,xii; CHI i; CHIS ii,xii (ADW); El Tuito, 5 km N xii (UCB); LCA v (MZFC); La Huerta, 7 mi E (AMNH); MIS i,ii,xii (ADW); MIS, 12 km S PV iv (LACM); PV vii (CAS), x (LACM); PV, 34 km S i; RT at Hwy 200 i; YEL viii (LACM); ZEN vii,ix (MZFC).

Phoebis neocypris virgo (Butl. 1870). ADJ (Rodríguez 1982), v,x,xi (CIB); AHU v,vi,viii,x (MZFC); Ameca (Vázquez 1951); BDH v,vi,ix,xii (López 1989); BES ii,vi (IMCyP, Abud 1987,1988); El Durazno, 6 mi E iv (SDNHM); LCA ii,iv,vi,ix,xi (MZFC); LCA, 10 mi S LCU; LCU (AMNH); PLM iii,vi,viii (MZFC); Río San Pedro (AMNH).

Phoebis philea philea (L. 1763). ADJ (Rodríguez 1982), vi,ix (CIB); AHU vi,viii,x (MZFC); BDN (AMNH); BDH ix (López 1989); BDT i,xii (ADW); BES v–x (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC i–xii (Beutelspacher 1982), viii (UCB), ix (Opler 1989); CHIS xii (ADW); LCA v,viii–xi (MZFC); LCA, 10 mi S LCU (AMNH); Melaque, 8 km N xii (UCB); MIS i–iv,xii (ADW); MIS, 12 km S PV iv (LACM); PLM viii,x (MZFC); PV viii (Comstock & Vázquez 1961), iv,viii,xii (ADW); RT at Hwy. 200 i (LACM); TEN (AMNH); YEL viii (LACM), xii (ADW); ZEN viii,ix (MZFC).

Phoebis sennae marcellina (Cr. 1777). ADJ (Rodríguez 1982), i,v–xi (CIB); AHU vi,x (MZFC); Ameca viii (AME); Autlán (AMNH); BDH v–ix (López 1989); BDT i,xii (ADW); BES vii–x (IMCyP, Abud 1987,1988); EBC i–xii (Beutelspacher 1982), vii (UCB), ix (Opler 1989); CHP (AMNH), x (LACM); CHIS i,xii (ADW); CHI, 2.5 km W, on Hwy 200 i (ADW); BHC (AMNH); Cuzalapa i (MZFC); LCA v,viii (MZFC); La Huerta, 7 mi E; La Venta (AMNH); MAG viii (AME); MIS i,iii,iv,xii (ADW), iv (LACM); Ocotlán viii,ix (AME); PLM viii (MZFC); PV ii,iv,vi,x,xii (LACM), viii (Comstock & Vázquez 1961), xii (CAS), i,iii,iv,xii (ADW); PV, 7 km S, on Hwy 200 iii; PV, 22 km S, on Hwy 200 iii,iv; PV, 30 km S, on Hwy 200 iv; PV, 60 km S, on Hwy 200 i (LACM) Río San Pedro (AMNH); RT at Hwy 200 i (LACM); TEN (AMNH); YEL ii,iv,viii (LACM), xii (ADW); ZEN v,viii,x,xi (MZFC).

Rhabdodryas trite trite (L. 1758). BDT i,xii (ADW); LCA xi (MZFC); MIS iv,xii (ADW);

PV, 30 km S, on Hwy 200 iii,iv; PV, 38 km S, on Hwy 200 iv (LACM); YEL xii (ADW).

Aphrissa statira jada (Butl. 1870). BDN (AMNH); BDH vi,viii (López 1989); BDT i,xii (ADW); EBC vii (UCB); CHIS xii (ADW); LCA v,ix–xi (MZFC); MIS i,iv,xii (ADW); RT at Hwy 200 i (LACM); TEN (AMNH); YEL xii (ADW).

Kricogonia lyside (Godart 1869). BDN; CHM (AMNH); EBC viii,x (Beutelspacher,1982); TEN (AMNH).

Abaeis nicippe (Cr. 1780). ADJ (Rodríguez 1982), viii (CIB); AHU iii (MZFC); Ameca ix (AME); BDH viii–xii (López 1989); BES vii,x (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC ii,viii (Beutelspacher 1982); CHIS i,xii (ADW); BHC (AMNH); LCA, 10 mi S LCU (AMNH); PV iv (LACM), viii (Comstock & Vázquez 1961), i,xii (ADW); Río San Pedro (AMNH); ZEN vi–ix (MZFC).

Pyrisitia dina westwoodi (Boisd. 1836). ADJ, 2 mi S (AMNH); AHU ii–vi,viii,x,xi (MZFC); Ameca ix (AME); BDH v–xii (López 1989); BDT i,xii (ADW); CHI, on Hwy 200 i; CHIS i,xii (ADW); GUA (USNM); LCA i,ii,iv,vii–ix,xi (MZFC); LCA, 10 mi S LCU; LCU, 7 mi S (AMNH); MIS i,iii,iv,xii (ADW); MIS, 12 km S PV iv,v (LACM); Pihuamo ix (SDNHM); PV viii (Comstock & Vázquez 1961), i,iii,xii (ADW); PV, 60 km S i (LACM); Río San Pedro (AMNH); RT at Hwy 200 i (LACM); ZEN v,vii–ix,xi (MZFC).

Pyrisitia lisa centralis (Herr.-Sch. 1864). ADJ (Rodríguez 1982), i,iv–xii (CIB); Ameca ix (AME); BDH vii–ix (López 1989); BES vii,ix,x (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC viii (Beutelspacher 1982); CHP x (LACM); BHC (AMNH); MIS i,xii (ADW); Puente Grande iv (COEE, Gibson & Carrillo 1959); PV viii (Comstock & Vázquez 1961), xii (CAS), iii,iv (ADW).

Pyrisitia nise nelphe (R. Feld. 1869). ADJ (Rodríguez 1982), v–xii (CIB); ADJ, 2 mi S (AMNH); AHU ii,iii,vi,viii (MZFC); BDN (AMNH); BDH v,xi,xii (López 1989); BDT i,xii (ADW); CHM (Rodríguez 1982, AMNH); EBC i,iii (Beutelspacher 1982), x (UCB), ix (Opler 1989); LCA vi,viii–xi (MZFC); MIS i,iv,xii (ADW); ECPE iii; PLM iii (MZFC); PV ii (LACM), xii (CAS), iii,iv (ADW); Río San Pedro (AMNH); RT at Hwy 200 i (LACM); TEN (AMNH); Bahía de Tenacatita i (LACM); Valle de Autlán; Villa Corona, 1 mi E (AMNH); YEL ii (LACM); ZEN vii,viii,xi (MZFC).

Pyrisitia proterpia proterpia (Fabr. 1775). ADJ (Rodríguez 1982), ix–xi (CIB); AHU v,vi,xi (MZFC); BDH iii-xi (López 1989); BDT xii (ADW); BES i–iv,ix–xi (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC vii,ix,x,xii (Beutelspacher 1982), vii,x (UCB), ix (Opler 1989); CHP x (LACM); CHIS i,xii (ADW); BHC (AMNH); LCU, 7 mi S (AMNH); GUA, 10 mi S viii; GUA, 10 mi SW viii (SDNHM); LCA i–iii,ix–xi (MZFC); LCA, 10 mi S LCU; La Huerta, 7 mi E (AMNH); LDC vii (CAS); Mirador (AMNH); MIS iv,xii (ADW); PLM iii,viii (MZFC); PV ix (AME), viii (Comstock & Vázquez 1961), xii (CAS), iii,iv,xii (ADW); Tequila xii (DGSV, Hernández, Martínez & Rodríguez 1981); ZEN vii,ix (MZFC).

Eurema albula celata (R. Feld. 1869). LCA, 10 mi S LCU (AMNH).

Eurema boisduvaliana (C. Feld. & R. Feld. 1865). AHU v,vi; ECAL iii (MZFC); BDN (AMNH); BDH viii–xi (López 1989); BDT i,xii (ADW); CHM (AMNH); EBC i,vi,ix,x (Beutelspacher 1982), ix (Opler 1989); CHIS i,xii (ADW); El Tuito viii (LACM); LCA i,ii,vi,viii,ix,xi (MZFC); LCA, 10 mi S LCU; La Huerta, 7 mi E (AMNH); ECLO iii (MZFC); MIS i,iii,iv,xii (ADW); MIS, 12 km S PV iv (LACM); PV (De la Maza 1987), viii (Comstock & Vázquez 1961), i,iv,xii (ADW); PV, 22 km S, on Hwy 200 iii; RT at Hwy. 200 i; TEN i (LACM); YEL xii (ADW); ZEN vi,viii, x,xi (MZFC).

Eurema daira (Godart 1819). ADJ (Rodríguez 1982), v–xii (CIB); ADJ, 2 mi S (AMNH); AHU ii, iii,v,vi,viii,xi (MZFC); AJI, nr. viii (CMNH); Valle de Autlán; BDN (AMNH); BDN, nr. xii (LACM); BDH i–xii (López 1989); BDT i,xii (ADW); BES i–xii (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC x (UCB), i,ii,ix,xii (Beutelspacher 1982), ix (Opler 1989); CHP x (LACM); CHIS i,xii; CHI, 2.5 km W, on Hwy 200 i (ADW); El Chante, 13.7 mi S iv (SDNHM); GUA (AMNH), vii (CAS), viii (CMNH, UCB), xii (USNM); GUA, 28 mi N viii (UCB); GUA, 90 mi N viii (SDNHM); Hwy 200, 1–4.5 mi E km 175.5 i (ADW); LCA i,ii,v–ix,xi (MZFC); LCA, 10 mi S LCU (AMNH); ECLC iii (MZFC); LCU; La Huerta, 7 mi E (AMNH); ECLO iii (MZFC);

La Resolana, 1 mi SW; La Venta (AMNH); LDC xii (LACM), vi (UCB), vii (CAS); MAG viii (AME); Melaque, 11 km N vii (UCB); Mirador (AMNH); MIS i–iv,xii (ADW); MIS, 12 km S PV iv (LACM); Ocotlán viii (CMNH); Plan de Barrancas (AMNH); ECPE iii (MZFC); PLM i,ii,iii,v,vi,x,xi (MZFC); PV ix (LACM), viii (Comstock & Vázquez 1961), x (USNM), xii (CAS); i,iii,iv,xii (ADW); PV, 21 km S, on Hwy 200 iii; PV, 22 km S, on Hwy 200 iii,iv; PV, 60 km S i; San Ysidro, GUA xii (LACM); TEN; Villa Corona, 1 mi E (AMNH); YEL xii (ADW); ZEN v,vi,vii,ix,xi (MZFC).

Eurema mexicana mexicana (Boisd. 1836). AHU vi,viii,xi; ECAL iii (MZFC); BDH vi,viii–xii (López 1989); BES viii,ix,x (IMCyP, Abud 1987,1988); CHP x (LACM); CHIS i,xii (ADW); ECET iii; LCA ii,ix,xi (MZFC); LCA, 10 mi S LCU (AMNH); ECLO iii (MZFC); LDC vii (CAS); PLM vi,viii,x,xi (MZFC); Sayula, 2 mi SE (AMNH); YEL xii (ADW).

Eurema salome jamapa (Reak. 1866). AHU viii,x,xi; ECAL iii (MZFC); Valle de Autlán (AMNH); BDN, nr. xii (LACM); BDH i,xii (López 1989); CHIS i (ADW); ECET III; LCA viii,ix,xi; ECLC iv; EC xii (MZFC); Mazamitla x (SDNHM); PLM i–iii,vi,viii,x,xi (MZFC); PV xii (CAS); ZEN x (MZFC).

Nathalis iole iole Boisd. 1836. ADJ (Rodríguez 1982), ii–iv,vi,ix,x (CIB); ADJ, 2 mi S (AMNH); AHU iii,vi,viii (MZFC); BDH i,vii–xii (López 1989); BES i,vi,viii,x,xi (IMCyP, Abud 1987,1988); CHM (AMNH); CHP ii (AME); BHC (AMNH); GUA vi,vii (CAS); LCU; La Huerta, 7 mi E (AMNH); LDC vii (CAS); Mirador (AMNH); ECPE iii; PLM x (MZFC); PV viii (Comstock & Vázquez 1961); Sayula, 1 mi SW; Villa Corona, 1 mi E (AMNH).

Hesperocharis costaricensis pasion (Reak. [1867]). ADJ (Rodríguez 1982), i,vi,ix (CIB); AHU x,xi (MZFC); BDH i,ii (López 1989); BDT i,xii (ADW); ELT iii (MZFC); GUA iv (AMNH); LCA xi (MZFC); MIS i,iv,xii (ADW); PLM v (MZFC).

Hesperocharis crocea jaliscana (Schaus 1898). ADJ (Rodríguez 1982), ii,vi,xii (CIB); GUA (Godm. & Sal. 1878–1901, USNM), v (AMNH).

Hesperocharis graphites avivolans (Butl. 1865). ECAL iii (MZFC).

Neophasia terlootii Behr 1869. Volcán de Colima (De la Maza 1987).

Catasticta flisa flisa (Herr.-Sch. [1858]). LCA xi (MZFC); LCU (AMNH); ECLO iii; ECPE iii; PLM iii,v,viii,x,xi (MZFC).

Catasticta nimbice nimbice (Boisd. 1836). ADJ (Rodríguez 1982), i–iii,xii (CIB); ECAL iii (MZFC); BDH iii (López 1989); BES i (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); CHP x (LACM); LCA xi; ECLO iii; EC iv (MZFC); Los Reyes iii (AMNH); Ocotlán v (CAS); ECPE iii; PLM iii,xi (MZFC).

Catasticta teutila teutila (Doubleday 1847). Arandas iv (COEE, Gibson & Carrillo 1959).

Pereute charops leonilae Llorente 1986. AHU x,xi (MZFC); El Chante, 11.6 mi S iv (SDNHM); LCA xi; ECLC iv; ECLO iii; PLM viii,x,xi (MZFC).

Melete lycimnia isandra (Boisd. 1836). AHU xi (MZFC); BDT i,xii (ADW); EBC ix (Beutelspacher 1982); LCA xi (MZFC); MIS i,iv,xii (ADW), x (USNM); PV (De la Maza 1987); PV, 60 km S i; RT at Hwy 200 i (LACM); TEN (AMNH); Tomilita ii (AME); ZEN vii,viii (MZFC).

Glutophrissa drusilla aff. ***tenuis*** Lamas 1981. AHU x (MZFC); BDN xi, xii (AMNH); BDN, nr. xii (LACM); BDH xi (López 1989); BDT i,xii (ADW); EBC vii,xi (UCB), viii,ix,x (Beutelspacher 1982); CHIS xii (ADW); BHC (AMNH); ELT iii (MZFC); LCA iv,vi,viii,ix,xi (MZFC); MIS i,iv,xii (ADW); PLM iii,xi (MZFC); PV viii (Comstock & Vázquez 1961), iii,xii (ADW); PV, 21 km S, on Hwy 200 iii; PV, 22 km S, on Hwy 200 iv; PV, 38 km S iv; PV, 60 km S i; Río San Nico iv; RT at Hwy 200 i (LACM); TEN (AMNH); YEL xii (ADW).

Pieris rapae rapae (L. 1758). ADJ (Rodríguez 1982), v,x,xi (CIB); Ameca viii (AME); BDH i–xii (López 1989); Estipac (De la Maza 1987); GUA iv (AMNH).

Pontia protodice (Boisd. & LeC. 1829). ADJ (Rodríguez 1982), ii–vii,xii (CIB); AHU iii (MZFC); BDH x–xii (López 1989); BES vi (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC viii (Beutelspacher 1982), vii (UCB).

Leptophobia aripa elodia (Boisd. 1836). ADJ (Rodríguez 1982), i,iii,vii (CIB); BDH i–xii (López 1989); BES i,x (IMCyP, Abud 1987,1988); CHP x (LACM); GUA vii (CAS),

viii (LACM, USNM), x (LACM), xii (AMNH); LCA ix–xi (MZFC); LDC xii (LACM); LDC, La Floresta ix (UCB); Lagos iv (COEE, Gibson & Carrillo 1959); Mazamitla x (SDNHM); ECPE iii; PLM x,xi (MZFC).

Pieriballia viardi laogore (Godm. & Sal. 1889). BDT xii (ADW); EBC iii,x,xii (Beutelspacher 1982), xii (UCB); CHIS i,xii (ADW); ELT iii (MZFC); LCA ii–iv,viii,ix,xi (MZFC); MIS i,xii (ADW); MIS, 12 km S PV iv (LACM); PLM iii,vi,viii,xi (MZFC); PV (De la Maza 1987), xii (CAS); RT at Hwy. 200 i (LACM); TEN iii,iv,xi,xii (AMNH); Bahía de TEN i (LACM); YEL xii (ADW).

Ascia monuste monuste (L. 1764). ADJ (Rodríguez 1982), i,v,vii–xi (CIB); AHU iii,v,vi,viii,xi (MZFC); Autlán vii (AMNH); BDN ix (USNM); BDH ix–xi (López 1989); BDT i,xii (ADW); CHM (Rodríguez 1982); EBC vii,viii (UCB), i–xii (Beutelspacher 1982), ix (Opler 1989); CHIS xii (ADW); BHC (AMNH); GUA viii (USNM); LCA v,viii,ix,xi (MZFC); LCA, 10 mi S LCU (AMNH); Melaque, 8 km N xii (UCB); MIS i,iii,iv,xii (ADW); MIS, 12 km S PV iv (LACM); PLM v,xi (MZFC); PV vii,xii (CAS), viii (Comstock & Vázquez 1961, LACM), i,iii,iv,xii (ADW); PV, 7 km S, on Hwy 200 iii; RT at Hwy 200 i (LACM); YEL xii (ADW); ZEN vi, vii (MZFC).

{***Ganyra howarthi*** (Dixey 1915)}. JAL (Beutelspacher 1986). This record is very questionable, for the nearest reliable records for this species are from near Los Mochis, Sinaloa. See Bailowitz (1988).

Ganyra josephina josepha (Salvin & Godman 1868). AHU xi (MZFC); BDN xi (AMNH); BDT i,xii; CHIS xii (ADW); Bahía de CHM iii,xii (AMNH); EBC i–xii (Beutelspacher 1982), vii,x,xii (UCB), ix (Opler 1989); LCA viii,ix,xi (MZFC); Melaque, 5 km N xii; Melaque, 8 km N xii (UCB); MIS i,iii,iv,xii (ADW); PLM viii,xi (MZFC); PV viii (Comstock & Vázquez 1961), i–iv,xii (ADW); PV, 21 km S, on Hwy 200 iii; RT at Hwy. 200 i (LACM); TEN xi (AMNH); YEL xii (ADW).

NYMPHALIDAE (158 SPECIES)

Dione juno huascuma (Reak. 1866). ADJ (Rodríguez 1982), viii (CIB); AHU xi (MZFC); BDH xii (López 1989); BDT i,xii (ADW); EBC xi (UCB), ix (Opler 1989); CHIS xii (ADW); ELT iii (MZFC); MIS i,iii,iv,xii (ADW); PLM ix (MZFC); PV (De la Maza 1987), xii (CAS), iii,iv (ADW); PV, 60 km S i (LACM).

Dione moneta poeyii Butl. 1873. ADJ (Rodríguez 1982), v,vi,viii–xi (CIB); AHU ii, xi (MZFC); BDH x–xii (López 1989); BES i,v,x,xi (IMCyP, Abud 1987,1988); CHP x (LACM); CHIS xii (ADW); LCA xi (MZFC); MIS xii (ADW); Ocotlán x (USNM); Parque Volcán de Fuego, 10.8 mi N iv (SDNHM); PLM i,iii,viii–xi (MZFC); RT at Hwy 200 i (LACM).

Agraulis vanillae incarnata (Riley 1926). ADJ (Rodríguez 1982), iii (CIB); AHU ii,xi (MZFC); BDH iv,ix (López 1989); BDT xii (ADW); BES ix (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC (Beutelspacher 1982), vii (UCB); CHIS xii (ADW); LCA ii,viii (MZFC); MIS i,iii,iv,xii (ADW); PV (De la Maza 1987), viii (Comstock & Vázquez 1961), iii,iv,xii (ADW); RT at Hwy 200 i (LACM); ZEN ix (MZFC).

Dryas iulia moderata (Riley 1926). AHU vi,viii,ix (MZFC); BDH x–xii (López 1989); BDT i,xii (ADW); EBC xii–iii (Beutelspacher 1982), vii (UCB); CHIS i,xii (ADW); LCA i,ix,xi (MZFC); Melaque, 5 km N xii (UCB); MIS i–iv,xii (ADW); MIS, 12 km S PV iv (LACM); PV (De la Maza 1987), viii (Comstock & Vázquez 1961), xii (CAS), i–iv,xii (ADW); PV, 22 km S, on Hwy 200 iv; PV, 60 km S i; RT at Hwy 200 i (LACM); YEL ii,iv (LACM), xii (ADW); ZEN xi (MZFC).

Heliconius charithonia vazquezae Comstock & Brown 1950. ADJ (Rodríguez 1982), iv,v (CIB); AHU v,vi,viii,ix,xi (MZFC); BDN, nr. xii (LACM); BDH i,vi,ix–xii (López 1989); BDT i,xii (ADW); BES x,xi (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC i–xii (Beutelspacher 1982), vii,xi (UCB), ix (Opler 1989); CHP x (LACM); CHI, on Hwy 200 i; CHIS i,xii (ADW); El Durazno, 6 mi E iv (SDNHM); El Tuito viii (LACM); GUA (De la Maza 1987); LCA i,ii,v,vi,viii,ix,xi (MZFC); Melaque, 5 km N xii; Melaque, 8 km N xii (UCB); MIS i–iv,xii (ADW), x (USNM); MIS, 12 km S PV iv (LACM); ECPE III; PLM iii,viii,ix (MZFC); PV ii,x (LACM), viii

(Comstock & Vázquez 1961), xii (CAS), i–iv,xii (ADW); PV, 7 km S, Hwy 200 iii (LACM); PV, 38.8 mi S vii (SDNHM); PV, 39 km S, on Hwy 200 i; PV, 60 km S i; RT at Hwy 200 i (LACM); YEL iv,viii (LACM), xii (ADW); ZEN ix (MZFC).

Heliconius erato punctata Beutelspacher 1992. BDN, nr. xii (LACM); BDH xii (López 1989); BDT i,xii; CHIS i,xii (ADW); MIS (Beutelspacher 1992), i–iv,xii (ADW); MIS, 12 km S PV iv; PV (Beutelspacher 1992), x (LACM), xii (CAS), i–iv,xii (ADW); PV, 12 km S, on Hwy. 200 i,iv,v,xii; RT at Hwy. 200 i; YEL viii (LACM).

Heliconius hortense Guérin [1844]. AHU xi; ELT iii; ECET iii; LCA xi; ECPE iii; PLM i,iii,v,vi,viii–xi (MZFC).

Heliconius ismenius telchinia Doubleday 1847. MIS, 12 km S PV iv (LACM).

Euptoieta claudia daunius (Herbst 1798). BDH viii (López 1989); PV viii (Comstock & Vázquez 1961).

Euptoieta hegesia hoffmanni Comstock 1944. ADJ (Rodríguez 1982), v,vi,ix–xii (CIB); AHU iii,vi,viii–x (MZFC); BDN, nr. xii (LACM); BDH iv–x (López 1989); BDT i,xii (ADW); BOL (Godm. & Sal. 1878–1901); BES i,iii–xii (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC vii-xii (Beutelspacher 1982), vii,x (UCB), ix (Opler 1989); CHP x (LACM); CHIS i,xii (ADW); El Tuito, 5 km N xii (UCB); Hwy 200, 1–4.5 km W km 175.5 i (ADW); LCA ii,iii,v,viii,ix (MZFC); Melaque vii (UCB); MIS i–iv,xii (ADW), x (USNM); MIS, 12 km S PV iv,v (LACM); PLM viii,ix,x,xi (MZFC); PV ii,iv,viii,x (LACM), viii (Comstock & Vázquez 1961), xii (CAS), i,iii,iv,xii (ADW); PV, 5.2 km S, on Hwy 200 i; PV, 7 km S, on Hwy 200 iii; PV, 60 km S i; RT at Hwy 200 i (LACM); Tizapán, 30 mi W vi (CAS); YEL iv (LACM), xii (ADW); ZEN vi,vi,ix,xi (MZFC).

Vanessa atalanta rubria (Frühstorfer 1909). ZEN vii (MZFC).

Cynthia annabella (Field 1971). BDH viii–xi (López 1989).

Cynthia cardui (L. 1758). BOL (Godm. & Sal. 1878–1901); PLM vi,xi; ZEN vii (MZFC).

Cynthia virginiensis (Drury 1773). ADJ (Rodríguez 1982), ix–xi (CIB); BES i,v,ix–xii (IMCyP, Abud 1987,1988); GUA vii (CAS); PLM vi,viii–x (MZFC).

Polygonia g-argenteum (Doubleday 1848). LCA ix (MZFC).

Nymphalis antiopa antiopa (L. 1758). ADJ (Rodríguez 1982), xi (CIB); AHU x (MZFC); BDH viii (López 1989); BES i,v,x (IMCyP, Abud 1987,1988).

Hypanartia godmani (Bates 1864). PLM x (MZFC).

Hypanartia lethe (Fabr. 1793). CHP (AMNH).

Anartia amathea fatima Fabr. 1773. ADJ (Rodríguez 1982), i,iv,vi–xi (CIB); AHU ii,iii,v,vi,viii,xi (MZFC); Valle de Autlán; BDN (AMNH); BDH ix–xi (López 1989); BDT i,xii (ADW); CHM (Rodríguez 1982); EBC i–xii (Beutelspacher 1982), vii,xi (UCB), ix (Opler 1989); CHIS i,xii (ADW); LCA (AMNH), i,ii,viii,ix,xi (MZFC); MIS i,iii,iv,xii (ADW); MIS, 12 km S PV iv (LACM); PV viii (Comstock & Vázquez 1961), ii,iv,vii–x (LACM), xii (CAS) i,iii,iv,xii (ADW); PV, 7 km S, on Hwy 200 iii; PV, 12 km S, on Hwy 200 iv; PV, 22 km S, on Hwy 200 iii; PV, 53 km S, on Hwy 200 i; PV, 60 km S i; RT at Hwy 200 i (LACM); TEN (AMNH); YEL ii,v,viii (LACM); ZEN v,vi,ix,xi (MZFC).

Anartia jatrophae luteipicta Frühstorfer 1907. ADJ (Rodríguez 1982), i,x (CIB); ADJ, 2 mi S (AMNH); AHU iii (MZFC); BDN (AMNH); BDH ix–xii (López 1989); BDT xii (ADW); BES i,v,viii–xi (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC i–xii (Beutelspacher 1982) vii (UCB); CHP x (LACM); CHIS i,xii (ADW); El Tuito vii (LACM); GUA, 9 mi N viii (SDNHM); LCA viii (MZFC); La Huerta, 7 mi E (AMNH); Melaque, 11 km N vii (UCB); MIS i,xii (ADW); PV (De la Maza 1987), viii (Comstock & Vázquez 1961), viii,ix,x (LACM), xii (CAS), ix,xii (ADW); TEN; Villa Corona, 1 mi E (AMNH); ZEN v–viii,xi (MZFC).

Siproeta epaphus epaphus (Latr. [1813]). AHU ix,xi (MZFC); BDN, nr. xii (LACM); BDH xii (López 1989); BDT i,xii (ADW); EBC i,vi–xii (Beutelspacher 1982); CHIS i,xii (ADW); LCA ii,ix,xi (MZFC); MIS i,iii,iv,xii (ADW); PLM x (MZFC); PV (De la Maza 1987), i,iii,iv,xii (ADW); RT at Hwy 200 i (LACM).

Siproeta stelenes biplagiata (Frühstorfer 1907). AHU iii,v,vi,viii,ix,xi (MZFC); BDH xii (López 1989); BDT xii; CHIS xii; CHI, 2.5 km W, on Hwy 200 i (ADW); EBC i,vi,xii (Beutelspacher 1982), vii,xi (UCB); BHC (AMNH); LCA i,ii,v,vi,vii–xi (MZFC); La

Huerta, 7 mi E (AMNH); Melaque, 11 km N vii; Melaque, 8 km N xii (UCB); MIS xii (ADW); MIS, 12 km S PV iv,v (LACM); PLM ix (MZFC); PV i,iii,v,ix (LACM), viii (Comstock & Vázquez 1961), xii (ADW); RT at Hwy 200 i (LACM); TEN (AMNH); ZEN viii,ix,xi (MZFC).

Junonia coenia Hübner [1822]. ADJ (Rodríguez 1982), vii (CIB); AHU ii,iii,viii,xi (MZFC); BDH xii (López 1989); BOL (Godm. & Sal. 1879–1901); BES i,iii,iv,viii–xii (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC i,xii (Beutelspacher 1982); LCA i,ii,v,vi,viii,xi (MZFC); ECLO iii; PLM iii (MZFC); ZEN vi (ADW).

Junonia genoveva nigrosuffusa B. & McD. 1916. ADJ (Rodríguez 1982), x (CIB); BDN, nr. xii (LACM); BDT i,xii; CHIS i,xii; Hwy 200, 1 km E km 175.5 i (ADW); MAG, 4 mi W x (UCB); MIS xii (ADW); PV ii,viii,ix, (LACM), viii (Comstock & Vázquez 1961), xii (CAS), iv (ADW); PV, 21 km S, on Hwy 200 iii; PV, 30 km S, on Hwy 200 iv; RT at Hwy 200 i (LACM); Río Verde, 17 mi S Yahualica, Hwy 116 ix; San José del Tajo ix (SDNHM); ZEN vi (ADW). Typical dark *nigrosuffusa* inhabits the higher elevations in western Mexico, while a pale subspecies of *genoveva* occurs along the coast from at least Sinaloa to northern Jalisco. Intergrades have been taken at intermediate elevations in Sinaloa and Jalisco (Puerto Vallarta, and 1 km E km 175.5 of Hwy 200, in Jalisco).

Chlosyne definita anastasia (Hemming 1934). ADJ (Rodríguez 1982), ii,v (CIB).

Chlosyne endeis endeis (Godm. & Sal. 1894). Sayula, 1 mi SW vii,viii (AMNH).

Chlosyne gloriosa Bauer 1960. BDN, nr. xii (LACM); Barra de Tomatlán (De la Maza 1987); BDH i,ix–xii (López 1989); BDT i,xii; CHIS xii (ADW); EBC viii,x (Beutelspacher 1982); MIS (De la Maza 1987), i,iii,iv,xii (ADW); PV (De la Maza 1987); PV, 17 mi N vii (SDNHM); PV, 34 km S i (LACM); RT at Hwy 200 i (LACM); TEN (Bauer 1960), xi,xii (AMNH).

Chlosyne hippodrome hippodrome (Geyer 1837). AHU v,viii,ix,x,xi (MZFC); BDH i (López 1989); BDT xii (ADW); LCA (AMNH), i,ii,viii–xi (MZFC); LCU, 7 mi S (AMNH); MIS i,iii,iv,xii (ADW), x (USNM); Pihuamo ix (SDNHM); PLM ix,x (MZFC); Río San Pedro (AMNH); ZEN viii,ix,xi (MZFC).

Chlosyne lacinia crocale (Edw. 1874). ADJ (Rodríguez 1982), ii,vi–xi (CIB); AHU x,xi (MZFC); BDH viii (López 1989); BES x (IMCyP, Abud,1987,1988); CHM (Rodríguez 1982); EBC x (Beutelspacher 1982), ix (Opler 1989); CHIS xii (ADW); GUA (Higgins 1960, USNM), viii,x,xi (LACM); LCA ix–xi (MZFC); LDC (Bauer, 1960); Ocotlán viii (CMNH); PLM x (MZFC); PV viii (LACM), i,xii (ADW); Río Verde, 17 mi S Yahualica, Hwy 116 ix (SDNHM); Tlaquepaque ix (USNM); ZEN viii,xi (MZFC).

Chlosyne marianna Röbert [1914]. TEN (AMNH).

Chlosyne marina dryope (Godm. & Sal. 1894). AHU x,xi (MZFC); Autlán, 20 mi SW vii (SDNHM); Barra de Tomatlán (De la Maza 1987); EBC x (Beutelspacher 1982); ELT vii (MZFC); GUA ix (Higgins 1960); LCA (AMNH), vii–ix,xi (MZFC); LCU, 7 mi S (AMNH); Puerto de Mazos, 9 mi SW Autlán x (CAS); PLM x,xi (MZFC); Río San Pedro (AMNH); YEL viii (LACM); ZEN viii (MZFC).

Chlosyne mazarum Miller & Rotger 1979. Barra de Tomatlán; MIS (De la Maza 1987).

Chlosyne riobalsensis Bauer 1961. Valle de Autlán vii,viii (AMNH); Barra de Tomatlán (De la Maza 1987); BDH x (López 1989); EBC vii (Beutelspacher 1982); MIS (De la Maza 1987); Río San Pedro vii,viii; Sayula, 1 mi SW vii,viii; TEN xi (AMNH).

Chlosyne rosita montana (Hall 1924). GUA (USNM); Río San Pedro vii,viii (AMNH).

Anemeca ehrenbergii (Geyer [1833]). ADJ (Rodríguez 1982), i–x (CIB); BDH x (López 1989); BOL (Godm. & Sal. 1878–1901); BES vii–ix,xi (IMCyP, Abud 1987,1988); CHP x (LACM); GUA (De la Maza 1987), iii,viii (USNM); LDC (Godm. & Sal. 1878–1901); Lagos ix (COEE, Gibson & Carrillo 1959), xi (DGSV, Hernández, Martínez & Rodríguez 1981); Ocotlán iv,x,xi (USNM); PLM viii, x (MZFC).

Thessalia cyneas cyneas (Godm. & Sal. 1878). GUA (Higgins 1960).

Thessalia theona ssp. AHU viii,xi (MZFC); BDN ii (Austin & Smith in litt.); BDT i,xii (ADW); BES xi (IMCyP, Abud 1987,1988); CHIS xii (ADW); EBC ii,vi,viii,x (Beutelspacher 1982), ix (Opler 1989); Hwy 200, 4.5 km W km 175.5 i (ADW); LCA ii,viii,xi (MZFC); LDC (Godm. & Sal. 1878–1901); MIS i,xii (ADW); PLM xi

(MZFC); PV vii,ix,xii (ADW), vii (LACM), viii (Comstock & Vázquez 1961); PV, 38.8 mi S vii (SDNHM); YEL viii (LACM); ZEN viii (MZFC).

Texola anomalus anomalus (Godm. & Sal. 1897). CHP (De la Maza 1987); LCA viii,ix,xi; ZEN vi,vi,xi (MZFC).

Texola elada elada (Hewit. 1868). ADJ, 2 mi S vii (AMNH); AHU ii,iii,v,viii–xi (MZFC); Valle de Autlán (AMNH); BDH vii–ix (López 1989); BES vii,viii,x,xi (IMCyP, Abud 1987,1988); CHP x (LACM); CHP Sur (AMNH); GUA (USNM); GUA, 8 mi N viii (UCB); GUA, 90 mi N viii (SDNHM); LCA (AMNH), i,ii,v,vii–ix,xi (MZFC); LCU, 7 mi S (AMNH); ECLO iii (MZFC); La Venta (AMNH); LDC (Godm. & Sal. 1878–1901, Higgins 1960), vii (SDNHM); Mirador vii (AMNH); Pte. Barranquitas, 14 mi NW MAG x (UCB); Tecolotlán, 5.5 mi NE vii (SDNHM); Tizapán, 30 mi W vi (CAS); Tlaquepaque x (CUIC); ZEN v–ix,xi (MZFC).

Microtia elva elva Bates 1864. AHU ii,ix,x (MZFC); Valle de Autlán; BHC (AMNH); BDH vi–ix (López 1989); BDT xii (ADW); CHM (AMNH); EBC iii,viii,x (Beutelspacher 1982), vii (UCB), ix (Opler 1989); CHIS xii (ADW); ELT iii (MZFC); GUA ix (LACM); LCA (AMNH), ii,v,viii–xi (MZFC); MIS i,xii (ADW); Pte. Barranquillas, 14 mi NW MAG x (UCB); PLM viii,ix (MZFC); PV ii,vi,x (LACM), iii,xii (ADW); PV, 12 km S, on Hwy 200 iv (LACM); PV, 17 mi N vii; PV, 21.7 mi S vii; PV, 38.8 mi S vii (SDNHM); YEL ii,viii (LACM), xii (ADW); ZEN vi–xi (MZFC).

Phyciodes mylitta thebais Godm. & Sal. 1878. Sayula, 2 mi SW vii,viii (AMNH).

Phyciodes pallescens (R. Feld. 1869). AHU iii (MZFC), vi (ADW); Valle de Autlán vii,viii (AMNH); BES i,ii,xi (IMCyP, Abud 1987,1988); CHM (Balcázar 1988); EBC iii,viii,x (Beutelspacher 1982); CHIS xii (ADW); GUA (Higgins 1981, USNM); LDC (Godm. & Sal. 1878–1901); MIS i,xii (ADW); Ocotlán viii (CMNH); PV xii (ADW); Villa Corona, 1 mi E vii,viii (AMNH); ZEN v (MZFC).

Phyciodes tharos distinctus Bauer 1975. ADJ, 2 mi S vii,viii (AMNH); BDH i,ix,xii (López 1989); Sayula, 2 mi SW vii,viii (AMNH); Tlaquepaque x (CUIC); Villa Corona, 1 mi E vii (AMNH).

Phyciodes vesta vesta (Edw. 1869). ADJ (Rodríguez 1982), vi–x,xii (CIB); AHU viii (MZFC); BOL (Godm. & Sal. 1878–1901); ECET iii; LCA v,viii (MZFC); LCA, 10 mi S LCU; LCU, 7 mi S (AMNH); ECLO, iii; ZEN viii (MZFC).

Anthanassa alexon alexon (Godm. & Sal. 1889). Arroyo Tlacuache, Camino Coamil v; Camino Cofradía-Cuzalapa viii; Cuzalapa; AHU ii–vi,viii,x,xi (MZFC); LCA (AMNH), i,ii,viii-xi (MZFC); LCU, 7 mi S (AMNH); ECLO iii (MZFC); MIS xii (ADW); ECPE iii; PLM ii,v,x,xi; ZEN viii (MZFC).

Anthanassa ardys ardys (Hewit. 1864). AHU iii,v,viii,x,xi (MZFC); BDT i, xii (ADW); Camino Coamil x; Cuatro Caminos v; Cuzalapa i,viii (MZFC); CHIS i,xii (ADW); El Terrero-El Sauz viii; ECET iv,v,xii (MZFC); LCA (AMNH), i,ii,iv,vi,viii–xi (MZFC); ECLC iii (MZFC); LCU (AMNH); LCU, 7 km S (AMNH); EC xii (MZFC); MIS i,iii,iv,xii (ADW); PLM i,ii,iii,v,vi,viii,x,xi (MZFC); PV, 39 km S, on Hwy 200 i (LACM); ECPE III; ZEN vii,viii,xi (MZFC).

Anthanassa argentea (Godm. & Sal. 1882). LCA, 10 mi S LCU vii,viii (AMNH).

Anthanassa drusilla lelex (Bates 1864). GUA (USNM); LCA i,ii (MZFC); PV viii (Comstock & Vázquez 1961).

Anthanassa frisia tulcis (Bates 1864). AHU ii,iii,v,vi,viii–x (MZFC); BDN xii (LACM); BDT i,xii (ADW); Bahía de CHM xii (AMNH); EBC ii–x (Beutelspacher 1982), ix (Opler 1989); CHIS i,xii (ADW); GUA (USNM); LCA i–iii,v,viii–x (MZFC); MIS i,iii,iv,xii (ADW); PV ii (LACM), viii (Comstock & Vázquez 1961), i,iii,iv,xii (ADW); PV, 17 mi N vii (SDNHM); PV, 53 km S, on Hwy 200 i; PV, 60 km S i; RT at Hwy 200 i (LACM); TEN iv,xii (AMNH); YEL ii,viii (LACM), xii (ADW); ZEN vii,xi (MZFC).

Anthanassa otanes otanes (Hewit. 1864). LCA iv,viii,x,xi; PLM v,x (MZFC).

Anthanassa ptolyca amator (Hall 1929). Cuzalapa i; AHU ii,iii,v,x,xi; LCA i,ii,vii–ix,xi; ECLC iii; ECLO iii; EC xii; ECPE iii; PLM ii,iii,x,xi; ZEN viii,xi (MZFC).

Anthanassa sitalces cortes (Hall 1917). El Floripondio, km 80 El Grullo-Ciudad Guzmán v; AHU x,xi; ECAL iii; LCA i,iv,viii,ix,xi; ECLO iii; EC xii; ECPE iii; PLM i,v,viii,x,xi; ZEN viii (MZFC).

Anthanassa texana texana (Edw. 1863). ADJ (Rodríguez 1982), i–v,vii–X (CIB); AHU i,iv (MZFC); BDH i–xii (López 1989); BES i,vi,vii,x (IMCyP, Abud 1987,1988); LCU (AMNH); Jaramillo viii (MZFC); LCA (AMNH); LDC (Godm. & Sal. 1878–1901); Ocotlán viii (CMNH); Río Verde, 17 mi S Yahualica, Hwy 116 ix (SDNHM); Tequila xii (DGSV, Hernández, Martínez & Rodríguez 1981).

Castilia griseobasalis (Röbert 1914). BDN, nr. xii (LACM); BDT i,xii; CHIS xii (ADW); LCA viii (MZFC); MIS i,iii,iv,xii (ADW); PV (De la Maza 1987); RT at Hwy 200 i (LACM).

Historis odius odius (Fabr. 1775). AHU x; PLM vi (MZFC, ADW); PV x (Comstock & Vázquez 1961).

Historis acheronta cadmus (Cr. [1775]). EBC ix (Opler 1989).

Smyrna blomfildia datis Frühstorfer 1908. ADJ (Rodríguez 1982), ix,x (CIB); AHU ii,iii,vi,viii–xi; ECAL iii (MZFC); BDH viii,ix (López 1989); BES vi,viii,ix,x (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC iii,vii–xii (Beutelspacher 1982), ix (Opler 1989); El Durazno, 2.3 mi E vi (SDNHM); LCA i,ii,vi,viii,ix,xi (MZFC); MIS iii,iv,xii (ADW); PLM v,vi,viii,ix (MZFC); PV (De la Maza 1987), x (Comstock & Vázquez 1961); ZEN vi,ix (MZFC).

Smyrna karwinskii Geyer [1833]. AHU x; ECAL iii; ECLC iii,iv; ECPE iii; PLM vi,ix; ZEN vii (MZFC).

Colobura dirce dirce (L. 1758). AHU viii (MZFC); BDH xii (López 1989); ELT iii (MZFC); EBC xii (Beutelspacher 1982); LCA i,iii,vi,viii–xi (MZFC); MIS i,iii,iv, xii (ADW); PV (De la Maza 1987), xii (ADW); RT at Hwy 200 i (LACM); YEL xii (ADW).

Biblis hyperia aganisa Boisd. 1836. AHU iii,viii (MZFC); BDT xii (ADW); EBC i–iii,x–xii (Beutelspacher 1982), vii (UCB); CHIS xii (ADW); ELT iii (MZFC); LCA i–iii,v,viii,xi (MZFC); MIS, 12 km S PV iv (LACM); PLM x (MZFC); PV (De la Maza 1987), xii (CAS); PV, 30 km S, on Hwy 200 iv (LACM); ZEN viii,ix,xi (MZFC).

Mestra dorcas amymone (Mén. 1857). AHU iii,vi,viii (MZFC); BES ii (IMCyP, Abud 1987,1988); EBC i,iii,viii,x (Beutelspacher 1982), vii (UCB); BHC (AMNH); LCA viii,xi (MZFC); LCU, 7 mi S (AMNH); Mirador (AMNH); ZEN viii,xi (MZFC).

Myscelia cyananthe cyananthe C. Feld. & R. Feld. 1867. CHM (De la Maza 1989, De la Maza & Turrent 1985); EBC i–xii (Beutelspacher 1982), vii (UCB), ix (Opler 1989); CHIS xii (ADW); LCA iii,vi,xi (MZFC); MIS i (ADW); TEN (Jenkins 1984).

Myscelia cyaniris alvaradia R. G. Maza & Díaz 1982. EBC vi–xii (Beutelspacher 1982); CHIS xii (ADW); PV (De la Maza 1987, De la Maza & Turrent 1985).

Myscelia ethusa ethusa (Doyère [1840]). EBC i,iii,viii (Beutelspacher 1982), ix (Opler 1989); MIS iv,xii; YEL xii (ADW).

Catonephele cortesi R. G. Maza 1982. MIS, 12 km S PV iv (LACM); PV (De la Maza 1987). See Jenkins (1985).

Eunica monima monima (Cr. 1782). BDT xii (ADW); EBC vii (Beutelspacher 1982); CHIS xii (ADW); ELT iii (MZFC); El Tuito, 5 km N vii (UCB); LCA v,vi,viii,ix,xi (MZFC); LCA, 10 mi S LCU (AMNH); MIS i,xii (ADW); PV iv (UCB); RT at Hwy 200 i; YEL viii (LACM).

Eunica tatila tatila (Herr.-Sch. [1855]). AHU viii,xi (MZFC).

Hamadryas amphinome mazai Jenkins 1983. ADJ (Rodríguez 1982), ix,x (CIB); AHU vi,viii,x (MZFC); BDH ix,viii (López 1989); EBC vii (UCB), ix (Opler 1989); LCU (Jenkins 1983); LCA i,iii,vi,viii–xi (MZFC); MIS xii (ADW); ZEN vi,vii (MZFC).

Hamadryas atlantis lelaps Godm. & Sal. 1883. AHU iii,vi,viii–xi (MZFC); Autlán (Jenkins 1983); BDH iv–ix (López 1989); BES x (IMCyP, Abud 1987,1988); EBC vii,x (Beutelspacher 1982); CHP (Jenkins 1983), x (LACM); Cocula (Jenkins,1983); ELT iii (MZFC); GUA (many); GUA, 21 mi N viii (CAS); LCA i–vi,viii,ix,xi (MZFC); MAG x (COEE, Gibson & Carrillo 1959); Tonalá (De la Maza 1987); ZEN vii,viii (MZFC).

Hamadryas februa ferentina (Godart [1824]). ADJ (Rodríguez 1982), ix–xi (CIB); AHU iv–vi,viii,ix,x,xi (MZFC); BDH iv–xii (López 1989); BDT xii (ADW); BES xi (IMCyP, Abud 1987,1988); CHM (many); EBC i–iii,vii–xii (Beutelspacher 1982), vii (UCB), ix (Opler 1989); ELT iii (MZFC); GUA (Jenkins 1983, USNM); LCA ii,iii,vi,viii–xi

(MZFC); MIS i,xii (ADW); Ocotlán (Jenkins 1983); PLM v,vi,ix,xi (MZFC); PV viii (Comstock & Vázquez 1961); RT at Hwy 200 i (LACM); ZEN vi,vi,ix,xi (MZFC).

Hamadryas feronia farinulenta (Frühstorfer 1916). BES viii,xi,xii (IMCyP, Abud 1987,1988).

Hamadryas glauconome glauconome (Bates 1864). EBC viii (Beutelspacher 1982), ix (Opler 1989); GUA ix (BMNH, Jenkins 1983); TEN x (Jenkins 1983); ZEN vi (MZFC).

Hamadryas guatemalena marmarice (Frühstorfer 1916). AHU vi,viii–xi (MZFC); BES vi,xi,xii (IMCyP, Abud 1987,1988); EBC xii (Beutelspacher 1982), ix (Opler 1989); ELT iii; ECET iii (MZFC); GUA (Jenkins 1983, De la Maza 1987); LCA iii,vi,viii,x,xi (MZFC); PV (Jenkins 1983); ZEN vi,vi,xi (MZFC).

Pyrrhogyra edocla edocla Dubleday [1848]. RT at Hwy 200 i (LACM).

Pyrrhogyra neaerea hypsenor Godm. & Sal. 1884. BDT xii (ADW); EBC iii,viii–xii (Beutelspacher 1982), ix (Opler 1989); ELT iii; LCA viii,xi (MZFC); PV (De la Maza & Turrent 1985); TEN (AMNH); ZEN xi (MZFC).

Temenis laothoe quilapayunia R. G. Maza & Turrent 1985. AHU xi (MZFC); BDN, nr. xii (LACM); EBC vii (UCB); CHIS xii (ADW); LCA viii,xi (MZFC), vi (ADW); MIS i,iii,iv,xii (ADW).

Epiphile adrasta escalantei Descimon & Mast 1979. AHU viii,x,xi (MZFC); BDN, nr. xii (LACM); BDH xii (López 1989); El Durazno, 6 mi E iv (SDNHM); LCA ix,xi (MZFC); LCU (AMNH, Jenkins 1986); ECPE iii; PLM v,xi; ZEN xi (MZFC).

Nica flavilla bachiana (R. G. Maza & J. Maza 1985). PV (De la Maza & Turrent 1985).

Dynamine dyonis Geyer 1837. LCA ix,viii (MZFC); LCA, 10 mi S LCU (AMNH); ZEN viii (MZFC).

Dynamine postverta mexicana D'Almeida 1952. ADJ (Rodríguez 1982), iii (CIB); BDN, nr. xii (LACM); BDT xii (ADW); CHM (Rodríguez 1982); EBC i–iii,x–xii (Beutelspacher 1982), x,xi (UCB), ix (Opler 1989); CHIS xii (ADW); LCA ix,xi (MZFC); LCU; LCU, 7 mi S (AMNH); MIS i,iii,iv,xii; PV iii,iv,xii (ADW); TEN (AMNH); ZEN viii (MZFC).

Diaethria asteria (Godm. & Sal. 1894). AHU viii,x,xi (MZFC); BDN, nr. xii (LACM); ELT iii; LCA viii,x,xi; PLM iii,viii (MZFC).

Cyclogramma bacchis (Doubleday [1849]). ADJ (Rodríguez 1982), x,xi (CIB); AHU ii,iii,viii,ix,x,xi (MZFC); BDH xii (López 1989); El Tuito (De la Maza & Turrent 1985); LCA xi; PLM x,xi; ZEN viii,ix,xi (MZFC).

Cyclogramma pandama (Doubleday [1849]). AHU iii,viii,x,xi; ECET xii (MZFC); El Tuito (De la Maza & Turrent 1985).

Adelpha basiloides basiloides (Bates 1865). BDT xii; CHIS xii (ADW); LCA iii,xi (MZFC); MIS i,iii,iv,xii (ADW); PLM iii,v,xi (MZFC), vi (ADW); PV xii (CAS), iv (ADW).

Adelpha bredowii eulalia (Doubleday [1848]). Autlán iii (De la Maza 1987); BES i,iii,iv,viii,ix (IMCyP, Abud 1987,1988); ECLO iii (MZFC).

Adelpha celerio diademata Frühstorfer [1913]. BDN, nr. xii (LACM); LCA iv; EC xi (MZFC); MIS i,xii (ADW); Pihuamo ix (SDNHM); PV x (Comstock & Vázquez 1961); PV, 53 km S, on Hwy 200 i (LACM).

Adelpha fessonia fessonia (Hewit. 1847). AHU iii–v (MZFC); BDT xii (ADW); CHM (AMNH); EBC i,ii,viii,x–xii (Beutelspacher 1982), ix (Opler 1989); ELT iii (MZFC); LCA iii,v,ix,xi (MZFC); MIS i,iv,xii (ADW), x (USNM); MIS, 12 km S PV iv,v (LACM); Pihuamo ix (SDNHM); PV ix (Comstock & Vázquez 1961), x (LACM), ix,xii (ADW); RT at Hwy 200 i (LACM); TEN iii (AMNH); YEL xii (ADW).

Adelpha iphiclus massilides Frühstorfer [1916]. Atenquique x (Beutelspacher 1976a); ELT iii; LCA iv,viii,ix,xi (MZFC); LCA, 10 mi S LCU (AMNH); MAG viii (AME); MIS x (USNM); Pihuamo ix (SDNHM); PV ix (Comstock & Vázquez 1961); YEL xii (ADW); ZEN xi (MZFC).

Adelpha ixia leucas Frühstorfer [1916]. LCA xi (MZFC).

Adelpha leuceria leuceria (Druce 1874). El Durazno, 6 mi E iv (SDNHM); LCA xi; PLM v,xi (MZFC), vi (ADW).

Adelpha naxia epiphicla Godm. & Sal. 1884. AHU iii; LCA v (MZFC); YEL ii (LACM); ZEN viii (MZFC).

Adelpha paroeca emathia (R. Feld. 1869). LCA xi (MZFC).

Adelpha phylaca phylaca (Bates 1866). BDN, nr. xii (LACM); CHIS xii (ADW); LCA ix,xi (MZFC); LCU, 7 km S (AMNH); MIS iii,iv,xii (ADW), x (USNM); PV iv,xii (ADW); RT at Hwy 200 i (LACM); YEL xii (ADW).

Adelpha serpa massilia (C. Feld. & R. Feld. 1867). Atenquique x (Beutelspacher 1976a); BDH i (López 1989); BDT i,xii (ADW); EBC i,x–xii (Beutelspacher 1982); CHIS xii (ADW); El Tuito (De la Maza 1987); MIS i,iii,iv,xii (ADW); MIS, 12 km S PV iv (LACM); PLM vi (ADW); PV (De la Maza 1987), ix (Beutelspacher 1976a, LACM), iv,xii (ADW); PV, 22 km S, on Hwy 200 iv; Río San Nico iv; RT at Hwy 200 i (LACM); YEL xii (ADW).

Basilarchia arthemis arizonensis (Edw. 1882). ADJ (Rodríguez 1982), viii,x (CIB); BDH viii,ix,x (López 1989); GUA iii (AMNH).

Marpesia chiron marius (Cr. 1780). AHU ii,iii,viii,xi (MZFC); BDN, nr. xii (LACM); BDH i,ix–xii (López 1989); BDT xii (ADW); EBC viii (Beutelspacher 1982), vii (UCB); CHIS xii (ADW); LCA ii,vi–ix,xi (MZFC); MIS i,iv,xii (ADW); MIS, 12 km S PV v (LACM); PV vii (CAS), viii (Comstock & Vázquez 1961), xii (CAS), iii,xii (ADW); RT at Hwy 200 i; YEL viii,xii (LACM); ZEN ix (MZFC).

Marpesia petreus tethys (Fabr. [1777]). ADJ (Rodríguez 1982), vii,viii,x,xi (CIB); AHU iii,viii,ix,xi (MZFC); BDH i,xi,xii (López 1989); BDT xii (ADW); CHM (Rodríguez 1982); EBC viii,ix (Beutelspacher 1982), vii,x (UCB), ix (Opler 1989); LCA ii,ix,xi (MZFC); MIS iii,iv,xii (ADW); MIS, 12 km S PV iv, v (LACM); PV ix (Comstock & Vázquez 1961), ix,x (LACM), vii (CAS), ix,xii (ADW); ZEN vi (MZFC).

Archaeoprepona demophon occidentalis Stoffel & Descimon 1974. BDT xii; MIS i,iii,iv,xii (ADW); PV (De la Maza 1987), iv (ADW).

Archaeoprepona demophoon mexicana Llorente, Descimon & Johnson 1993. AHU iii,xi (MZFC, Llorente et. al. 1993); EBC i,xi (Beutelspacher 1982); LCA v,viii,x,xi (MZFC, Llorente et. al. 1993); PV (De la Maza 1987).

Prepona laertes octavia Frühstorfer 1905. PLM v (MZFC); Zapotlanejo (De la Maza 1987).

Zaretis callidryas (R. Feld. 1869). LCA iii,viii,x,xi (MZFC); TEN (AMNH).

Zaretis itus anzuletta Frühstorfer 1909. AHU viii,x; LCA ii,iii,v,vi,viii–xi (MZFC); MIS iii (ADW); PV x (Comstock & Vázquez 1961).

Siderone syntiche syntiche Hewit. [1854]. AHU xi (MZFC); EBC x–xii (Beutelspacher 1982); LCA iii,v,vi,viii,xi (MZFC); MIS xii (ADW); PV (De la Maza 1987).

Hypna clytemnestra mexicana Hall 1917. CHM (De la Maza 1987, AMNH); EBC i,ii,vii–xii (Beutelspacher 1982), x (DGSV, Hernández, Martínez & Rodríguez 1981), vii,x (UCB), ix (Opler 1989); LCA x (MZFC); TEN (AMNH); ZEN vii (MZFC).

Anaea troglodyta aidea (Guérin [1844]). ADJ (Rodríguez 1982), viii,ix,xi (CIB); AHU ii,iv,vi,viii,x,xi (MZFC); Valle de Autlán (AMNH); BDH iv–xii (López 1989); BDT xii (ADW); BES i,ii,iv–ix (IMCyP, Abud 1987,1988); CHM (De la Maza 1987); EBC i,vii–xii (Beutelspacher 1982), vii (UCB), ix (Opler 1989); ELT iii; LCA i–iv,vi,viii,ix,xi; ECLC iv (MZFC); LCU, 7 mi S (AMNH); ECLO iii (MZFC); Mazamita, 4 mi W (AMNH); Mazamitla x (SDNHM); PLM i,x (MZFC); PV x (Comstock & Vázquez 1961); TEN (AMNH); ZEN vi–ix (MZFC).

Consul electra castanea Llorente & Luis 1992. MIS iii (ADW); PV (De la Maza 1987), xii (CAS).

Consul fabius cecrops (Doubleday [1849]). LCA xi (MZFC); MIS i,iii,iv,xii (ADW); PV (De la Maza 1987); TEN (AMNH).

Fountainea eurypyle glanzi (Rotger, Escalante & Coronado 1965). CHIS xii (ADW); ELT iii; LCA ii,iv,vi,vii,viii,x,xi (MZFC); MIS iii (ADW), x (USNM); PLM vi (MZFC).

Fountainea glycerium glycerium (Doubleday [1849]). AHU viii,x,xi (MZFC); EBC vii (Beutelspacher 1982), ix (Opler 1989); LCA v,x,xi; ECLC iv (MZFC); LCU (AMNH); PLM viii,x,xi (MZFC).

Fountainea tehuana (Hall 1917). Arroyo Madera (De la Maza 1987); Bahía de CHM xii

(AMNH); CHM (De la Maza 1987); EBC i,ii,vii–x (Beutelspacher 1982); TEN xi (AMNH).

Memphis forreri (Godm. & Sal. 1884). AHU vi (MZFC); CHM xii (AMNH); EBC vii–xii (Beutelspacher 1982); ELT iii (MZFC); LCA iii,v (MZFC); PV (De la Maza 1987).

Memphis pithyusa (R. Feld. 1869). AHU x (MZFC); CHM (AMNH); EBC vii,viii,xii (Beutelspacher 1982), ix (Opler 1989); LCA iii-v,viii,xi; PLM v,vi,x,xi (MZFC); TEN (AMNH).

Asterocampa idyja argus (Bates 1864). AHU viii,xi; LCA iii,viii,ix,xi (MZFC); LCA, 10 mi S LCU (AMNH); MIS iii (ADW); PLM xi (MZFC); RT at Hwy 200 i (LACM); ZEN viii,xi (MZFC). See Friedlander (1987).

Doxocopa laure acca (C. Feld. & R. Feld. 1867). AHU iii,vi,viii–xi (MZFC); Valle de Autlán vii (AMNH); BDT i,xii (ADW); CHM (De la Maza 1987); EBC ix–xii (Beutelspacher 1982), xi (UCB), ix (Opler 1989); CHIS i,xii (ADW); LCA viii,ix,xi (MZFC); LCU i (AMNH); MIS i,iii,iv,xii (ADW); PLM viii,ix,xi (MZFC); PV (De la Maza 1987), x (Comstock & Vázquez 1961, USNM), xii (CAS), iii,iv,x,xii (ADW); TEN xi,xii (AMNH); ZEN ix,viii,xi (MZFC).

Doxocopa pavon theodora (Lucas 1857). PV (De la Maza 1987); TEN xi (AMNH).

Pessonia polyphemus polyphemus Westw. 1851. ADJ (Rodríguez 1982), iv–x (CIB); AHU vi,ix,x (MZFC); Valle de Autlán vii,viii; BHC; BDN xi (AMNH); BDN, nr. xii (LACM); BDH iv,ix–xii (López 1989); BES vi,ix,x (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982), x,xi (AMNH); EBC x–xii (Beutelspacher 1982), vii,xi (UCB); CHIS i; CHI, 2.5 km W, on Hwy 200 i (ADW); GUA vi (UCB); LCA vi,xi (MZFC); LCA, 10 mi S LCU vii,viii (AMNH); MIS i (ADW); Pte. Barranquitas, 18 mi NW MAG x (UCB); Puente Grande iv (COEE, Gibson & Carrillo 1959); PLM vi,ix,x (MZFC); TEN xi,xii (AMNH); YEL xii (ADW); ZEN vi,viii,ix (MZFC).

Opsiphanes boisduvalii Doubleday [1849]. ADJ (Rodríguez 1982), ii,x (CIB); AHU vi,x (MZFC); BDH i–xii (López 1989); BES iii (IMCyP, Abud 1987,1988); ELT iii; LCA iii,vi,ix–xi (MZFC); PV (De la Maza 1987), iii,xii (ADW).

Opsiphanes invirae fabricii (Boisd. 1870). CHM (De la Maza 1987); LCA iii,xi (MZFC); MIS iv,xii (ADW); PV viii (Comstock & Vázquez 1961), viii,x (LACM), i,iii,iv,xii (ADW).

Opsiphanes tamarindi C. Feld. & R. Feld. 1861. PV (De la Maza 1987).

Danaus eresimus montezuma Talbot 1943. AHU iii,viii,xi (MZFC); BDH v (López 1989); BDT i,xii (ADW); EBC i–xii (Beutelspacher 1982), ix (Opler 1989); LCA v,viii (MZFC); MIS i,iv,xii (ADW); MIS, 12 km S PV iv (LACM); Ocotlán viii (USNM); PV xii (CAS); RT at Hwy 200 i (LACM); ZEN vii,viii (MZFC).

Danaus gilippus thersippus (Bates 1863). ADJ (Rodríguez 1982), i,ii,v–viii,x–xii (CIB); AHU vi (MZFC); BDH v–ix (López 1989); BDT xii (ADW); BES ii,vii–xi (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC i–xii (Beutelspacher 1982), x,xi (UCB), ix (Opler 1989); CHP x (LACM); CHIS xii (ADW); GUA (De la Maza 1987); MIS i,iv,xii (ADW); PV ii,iv,viii,x (LACM), viii (Comstock & Vázquez 1961), xii (CAS); Tizapán, 30 mi W vi (CAS); YEL viii (LACM); ZEN v,vi (MZFC).

Danaus plexippus plexippus (L. 1758). ADJ (Rodríguez 1982), i,iii,v–vii,x,xii (CIB); AHU iii,viii,ix (MZFC), vi (ADW); BDH iv,x (López 1989); BDT xii (ADW); BES iv,v,ix,x (IMCyP, Abud 1987,1988); CHM (Rodríguez 1982); EBC xii (Beutelspacher 1982); MIS i,xii (ADW); Puente Grande iv (COEE, Gibson & Carrillo 1959); PLM ix (MZFC); PV viii (Comstock & Vázquez 1961); ZEN xi (MZFC).

Lycorea halia atergatis Doubleday [1847]. AHU iii,xi (MZFC); EBC xii (Beutelspacher 1982); Vertiente del Pacífico en CHM (Balcázar 1988); CHIS i,xii (ADW); LCA v,vi,x,xi (MZFC); MIS i,xii (ADW); PLM viii (MZFC); PV (De la Maza 1987), xii (ADW); TEN xi (AMNH).

Anetia thirza thirza Geyer [1833]. ECET iii,xi; ECLO iii; ECPE iii; PLM xi (MZFC).

Melinaea ethra flavicans C. C. Hoffmann 1924. CHM (De la Maza 1987); CHIS i (ADW); LCA v,ix,xi (MZFC); MIS xii (ADW); PV (De la Maza 1987); YEL xii (ADW). See Fox & Real (1971).

Oleria zea diazi J. Maza & Lamas 1978. GUA vi (CAS).

Pteronymia cotytto (Guérin [1844]). Bahía de TEN i (LACM).

Pteronymia rufocincta (Salvin 1869). Cuatitlán, 11.2 mi E, 4 mi E El Durazno viii (SDNHM); ECET iii; LCA xi; EC xii; PLM v,viii,x,xi (MZFC).

Greta morgane morgane (Geyer 1837). Autlán, 20 mi SSE vii (SDNHM); BDH xi (López 1989); CHIS i (ADW); ECET iii; LCA vii–ix,xi (MZFC); MIS i,xii (ADW); PLM x,xi (MZFC); PV (De la Maza, 1987).

Greta annette moschion (Godman 1901). ECET iii; EC iv; PLM x,xi (MZFC).

Episcada salvinia portilla J. Maza & Lamas 1978. LCA vi; PLM vi,ix (MZFC).

Libytheana carinenta mexicana Michener 1943. AHU iii,iv,viii–xi (MZFC); BDH xii (López 1989); CHP ix (USNM); EBC ix,x (Beutelspacher 1982); CHP (USNM); GUA (USNM); LCA iv,vi,xi (MZFC); PV ix (Comstock & Vázquez 1961); ZEN vii–ix,xi (MZFC).

Cissia cleophes (Godm. & Sal. 1889). LCU, 7 mi S (AMNH).

Cyllopsis caballeroi Beutelspacher 1982. CHIS xii (ADW); LCA xi (MZFC); MIS iv,xii (ADW); Paraíso, PV viii [Type Locality](Beutelspacher 1982, Miller & J. De la Maza 1984). A record for the very similar *Cyllopsis pephredo* (Godman, 1901) by Abud (1987, 1988) probably represents *caballeroi,* since *pephredo* is unknown from the region.

{***Cyllopsis gemma gemma*** (Hübner 1808)}. BDH ii–v (López 1989). This species was not reported to occur in western Mexico by Miller in 1974, and until specimens are seen to confirm this record, this species is listed as hypothetical for Jalisco.

Cyllopsis hedemanni hedemanni R. Feld. 1869. LCA xi (MZFC).

Cyllopsis henshawi hoffmanni (Edw. 1876). BOL (Godm. & Sal. 1878–1901).

Cyllopsis nayarit R. Chermock 1947. GUA (USNM, Miller 1974).

Cyllopsis suivalenoides Miller 1974. ECET iv; LCA iv,xi (MZFC); LCU (AME, Miller 1974); ECLO iii; EC xii; ECPE iii; PLM iii,v,vi,x,xi (MZFC).

Cyllopsis suivalens escalantei Miller 1974. ECPE iii (MZFC).

Dioriste tauropolis (Westw. [1850]). PLM iii,v,vi,x,xi (MZFC).

Eryphanis aesacus aesacus (Herr.-Sch. 1850). Ocotlán vi (CAS).

Euptychia fetna Butl. 1870. AHU viii,ix (MZFC); Autlán, 20 mi SW vii (SDNHM); BDH vii (López 1989); GUA (USNM); LCA vii,ix–xi (MZFC); LCA, 10 mi S LCU vii,viii (AMNH); LCU, 7 mi S (AMNH); ZEN vii,viii (MZFC).

Forsterinaria polyphemus cyclops (Butl. 1866). BES ii,vi (IMCyP, Abud 1987,1988).

Gyrocheilus patrobas patrobas (Hewit. 1862). Volcán de Colima (De la Maza 1987).

Hermeuptychia hermes (Fabr. 1775). ADJ (Rodríguez 1982), i–iii,v,viii,x,xi (CIB); AHU ii,iii,vi,viii–xi (MZFC); CHM (Rodríguez 1982); EBC ix–xii (Beutelspacher 1982); CHIS xii (ADW); ELT iii (MZFC); LCA i,ii,vi,ix,xi (MZFC); MIS xii (ADW); PV viii (Comstock & Vázquez 1961), xii (CAS), i,iii,iv,xii (ADW); ZEN v–vii,ix,xi (MZFC). More than one species may be represented by these records.

Megisto pellonia (Godman 1901). BOL; CHP (Godm. & Sal. 1878–1901).

Megisto rubricata pseudocleophes Miller 1976. AHU iv (MZFC); BES iv–vi,viii–x (IMCyP, Abud 1987,1988).

Pindis squamistriga R. Feld. 1869. ADJ (Rodríguez 1982), vii,xi (CIB); AHU vi,ix (MZFC); BDH i–v,xii (López 1989); BES i–vi,ix–xii (IMCyP, Abud 1987,1988); GUA (AMNH), viii (AME, Miller 1978); LCA ii,iv,vi,viii,xi (MZFC); LCU (AMNH, Miller 1978); LDC (Godm. & Sal. 1878–1901), x (LACM); MAG, 8.7 mi W viii (AME, Miller 1978); PLM iii,vi,viii,ix,x; ZEN ix (MZFC).

Manataria maculata (Hopffer 1874). ADJ (Rodríguez 1982), x (CIB); Ameca viii (AME); BDH viii (López 1989); BES vi,viii–x,xii (IMCyP, Abud 1987,1988); ECLC iv (MZFC); LCU ix (AMNH); PLM viii,x (MZFC).

Paramacera xicaque xicaque (Reak. [1867]). BOL (Godm. & Sal. 1878–1901); El Floripondio, km 80 El Grullo-Ciudad Guzmán iii; Las Capillas v (MZFC).

Pedaliodes dejecta ssp. PLM vi (MZFC, ADW).

Taygetis mermeria griseomarginata Miller 1978. ELT x; LCA iv,vi; EC ii; ECPE xi (MZFC).

Taygetis uncinata Weymer 1907. AHU vi; ELT x; LCA vi,viii–xi (MZFC); GUA (CUIC); MIS i,xii (ADW); PV, 60 km S i (LACM); Paraíso, PV viii (AME).

Taygetis weymeri Draut 1912. ECET iii (MZFC); Hwy 200, 2 km E km 175.5 i (ADW); LCA iv,vi; ECLC iv; ECLO iii; EC iv; PLM viii,x (MZFC).
Vareuptychia similis (Butl. 1867). EBC vi,vii (Beutelspacher 1982), ix (Opler 1989); CHIS xii (ADW); GUA (CUIC); Hwy 200, 2 km E km 175.5 i (ADW); LCA xii (AMNH); MIS iv,xii (ADW); PV viii (Comstock & Vázquez 1961).
Vareuptychia themis (Butl. 1867). AHU ii,iii,v,vi,xi; ECAL iii; ELT iii; LCA i–vii,ix–xi; PLM ii,iii,v,vi,ix,x (MZFC); PV viii (Comstock & Vázquez 1961); ZEN vi,vi,ix,xi (MZFC).
Vareuptychia undina (Butl. 1870). AHU viii,ix; LCA viii,ix; ZEN ix (MZFC).

LYCAENIDAE (136 SPECIES)

Euselasia eubule (R. Feld. 1869). AHU xi (MZFC); CHIS ii,xii (ADW); RT at Hwy 200 i (LACM).
Euselasia aurantiaca (Sal. & Godm. 1868). PLM xi (MZFC).
Mesosemia lamachus (Hewit. 1857). CHIS xii; MIS i (ADW).
Eurybia lycisca Westw. [1851]. GUA (USNM).
Eurybia halimede elvina Stichel 1910. LCA vi (ADW), viii,ix,xi (MZFC); MIS xii (ADW).
Napaea umbra umbra (Boisd. 1870). CHIS i,xii (ADW); LCA xi (MZFC); MIS xii (ADW); PV, 21.7 mi S vii (SDNHM).
Rhetus arcius beutelspacheri Llorente 1987. AHU viii,x,xi (MZFC); BDH i (López 1989); LCA viii,ix,xi (MZFC); LCA, 10 mi S LCU (AMNH, Llorente 1987); ZEN xi (MZFC).
Calephelis acapulcoensis McAlpine 1971. CHM iii (AMNH).
Calephelis fulmen Stichel 1910. BDT xii; CHIS xii (ADW); LCA, 10 mi S LCU vii,viii (AMNH); MIS xii (ADW); PV (Comstock & Vázquez 1961); TEN xi (AMNH).
Calephelis matheri McAlpine 1971. Sayula, 2 mi S vii,viii (AMNH); AJI xii (CMNH, McAlpine 1971); Bahía de CHM xi (AMNH); PV iv (ADW).
Calephelis mexicana McAlpine 1971. CHIS xii; MIS i,xii; PV xii (ADW).
Calephelis montezuma McAlpine 1971. BDT xii; MIS i,xii (ADW).
Calephelis nemesis nemesis (Edw. 1871). PV ix (Comstock & Vázquez 1961).
Calephelis perditalis perditalis B. & McD. 1918. BDH i–xii (López 1989). Despite McAlpine's revision of *Calephelis* in 1971, it is still nearly impossible to identify positively many specimens, and all *Calephelis* records presented here should be considered tentative.
Caria ino ino Godm. & Sal. 1866. BDT xii (ADW); ZEN viii (MZFC).
Caria stillaticia Dyar 1912. AHU viii,x; LCA viii,ix,xi (MZFC); LCA, 10 mi S LCU vii,viii; TEN xi (AMNH); ZEN viii (MZFC).
Baeotis zonata simbla (Boisd. 1870). AHU viii,x (MZFC); BDT xii (ADW); CHP x (LACM); CHIS xii (ADW); ELT iii; LCA viii,ix,xi (MZFC); MIS iv,xii; PV xii (ADW); ZEN viii (MZFC).
Lasaia sula sula Staud. 1888. BDH vii,viii (López 1989); LCA ix (MZFC); TEN xi (AMNH).
Lasaia agesilas callaina Clench 1972. AHU x; LCA x (MZFC); LCA, 10 mi S LCU (AMNH); TEN ix (AMNH, Clench 1972).
Lasaia maria maria Clench 1972. AHU viii–xi (MZFC); AJI vii,viii,x,xii (CMNH, Clench 1972); LCA viii,ix,xi (MZFC); LCU, 7 mi S (AMNH, Clench 1972); MIS xii (ADW); ZEN xi (MZFC). Beutelspacher recorded *Lasaia meris* (Cr., 1781) from Estación de Biología Chamela, xii but this record apparently refers to *maria*.
Exoplisia aff. ***cadmeis*** (Hewit. [1866]). LCA vi (ADW, MZFC); LCA, 10 mi S LCU vii,viii (AMNH).
Melanis cephise cephise (Mén. 1855). ADJ iv,vii–x (CIB); AHU viii (MZFC); Bahía de CHM xii (AMNH); BDN xi (AMNH); BDH i,vii–xii (López 1989); BDT xii (ADW); CHM (Rodríguez 1982); EBC i,vii (Beutelspacher 1982); CHP v (AMNH); GUA (White et. al. 1989, USNM); MIS xii (ADW); PV (Comstock & Vázquez 1961), ii (LACM), viii (USNM), xii (ADW); PV, 17 mi N vii (SDNHM); PV, 22 km S, on Hwy

200 iv; PV, 39 km S, on Hwy 200 i; PV, 60 km S i; Río San Nico iv; RT i (LACM); TEN xi (AMNH); Tomatlán Junction viii (SDNHM).

Melanis pixe sexpunctata J. White, A. White, & L. White 1989. AHU i,iii,v,vi,viii,x,xi (MZFC); BDN xi (AMNH); BDT xii (ADW); EBC x,xii (Beutelspacher 1982); LCA iv,viii,x (MZFC); MIS i,xii (ADW); MIS, 12 km S PV iv (LACM); PV ix (Comstock & Vázquez 1961; LACM), xii (ADW); PV, 12 km S, on Hwy 200 iv; PV, 22 km S, on Hwy 200 iv; PV, 39 km S, on Hwy 200 i; PV, 60 km S i; RT at Hwy 200 i (LACM); TEN xi (AMNH); ZEN vii,viii,xi (MZFC).

Anteros carausius carausius Westw. [1851]. AHU vi; BDT xii (ADW); CHM (De la Maza 1976); EBC xii (Beutelspacher, 1982); LCA xi (MZFC); PV (De la Maza 1976), ix (LACM), xii (ADW); PV, 17 mi N vii (SDNHM).

Calydna sturnula hegias R. Feld. 1869. PLM x (MZFC).

Emesis ares ares (Edw. 1882). AHU x (MZFC); AJI viii (CMNH); ECET iv; ECLC iii; PLM x,xi; ZEN viii (MZFC).

Emesis mandana furor Butl. & Druce 1872. AHU ix,x (MZFC); BDT xii; CHIS xii (ADW); ELT iii (MZFC); MIS iv,xii; PV xii (ADW).

Emesis vulpina Godm. & Sal. 1886. AHU vi (ADW); Bahía de CHM iii (AMNH); BDN xi (AMNH); BDT i,xii (ADW); CHM iii,xii (AMNH); EBC x,xii (Beutelspacher 1982); MIS i,xii (ADW); PV (Comstock & Vázquez 1961); TEN xi (AMNH).

Emesis poeas Godm. & Sal. 1901. AHU ii,iv,vi,viii,x (MZFC); LCA vi; ZEN vi (ADW), vii,viii (MZFC).

Emesis tenedia tenedia C. Feld. & R. Feld. 1861. AHU iii,v,viii,x,xi (MZFC); AJI ix (CMNH); ECAL iii (MZFC); BDT i,xii (ADW); CHP ii (CMNH); CHIS xii (ADW); El Chante, 13.7 mi S iv (SDNHM); ECET iv; ECLO iii; EC iv,ix (MZFC); MIS i,iii,iv,xii (ADW); Nuevo Necaxa iv (AME); ECPE iii; PLM iii,v,x,xi (MZFC); PV xii (ADW); ZEN xi (MZFC).

Emesis emesia emesia (Hewit. 1867). AHU viii,x,xi (MZFC); BDT xii (ADW); CHM iii (AMNH); EBC x,xii (Beutelspacher 1982), ix (Opler 1989); ELT iii; LCA viii,ix,xi (MZFC); MIS i,xii; PV xii (ADW); PV, 39 km S, on Hwy 200 i (LACM).

Pseudonymphidia clearista (Butl. 1871). Bahía de CHM iii (AMNH).

Apodemia hypoglauca hypoglauca (Godm. & Sal. 1878). AHU vi,viii,x,xi (MZFC); AJI viii,ix (CMNH); ELT iii (MZFC); LCA vi (ADW),viii–xi; ZEN vi,vi,xi (MZFC).

Apodemia walkeri Godm. & Sal. 1886. AJI vii–ix,xi,xii (CMNH); BDH i,vii (López 1989); EBC ix–xii (Beutelspacher 1982); CHP ii (CMNH); LDC, orilla S, km 86 viii (CMNH); Ocotlán x (USNM); PV xii (ADW).

Thisbe lycorias lycorias (Hewit. [1853]). CHM xii; BDN iii,iv,xi (AMNH); Tonilá vii (SDNHM).

Synargis mycone (Hewit. 1865). EBC ix (Beutelspacher 1982); LCA viii,xi (MZFC).

Calospila zeurippa Boisd. 1836. MIS ii (A. Hoare, pers. comm., 1995).

Pandemos godmanii Dewitz 1877. Cihuatlán vi (AME).

Theope virgilius virgilius (Fabr. 1793). MIS xii (ADW); RT at Hwy 200 i (LACM).

Theope eupolis Schaus 1890. BDT xii; CHIS xii; MIS i,iii,iv,xii (ADW); TEN xi (AMNH).

Theope diores Godm. & Sal. 1897. CHM iii (AMNH); EBC x–xii (Beutelspacher 1982); LCA v,xi (MZFC); PV (De la Maza 1987). Some of these records may refer to *eupolis* or *virgilius*. The status of these three taxa is still uncertain.

Theope publius C. Feld. & R. Feld. 1861. MIS xii (ADW).

Eumaeus toxea (Godart 1824). Autlán x (CIB); LCA ii,vi,xi (MZFC); MIS i (ADW); ZEN vi (MZFC).

"***Thecla***" (***busa*** group) ***busa*** (Godm. & Sal. 1887). LCA ix (MZFC).

"***Thecla***" (***hyas*** group) ***tolmides*** (Feld. & Feld. 1865). El Zarzamoro v (MZFC).

"***Thecla***" (***hyas*** group) nr. ***tolmides*** (Feld. & Feld. 1865). EC iv (MZFC).

Micandra furina (Godm. & Sal. 1887). ECPE iii (MZFC).

Evenus regalis (Cr. 1776). BDH vii–XI (López 1989); MIS, 12 km S PV iv (LACM); YEL xii (ADW).

"***Thecla***" (***gibberosa*** group) ***erybathis*** (Hewit. 1867). ECET iv; EC iv; ECPE iii (MZFC).

Allosmaitia strophius (Godart 1824). AJI xii (CMNH); LCA ix (MZFC).

Pseudolycaena damo (Druce 1875). AHU iii (MZFC); BDT xii (ADW); CHIS xii (ADW); EBC ix (Opler 1989); LCA vi,xi (MZFC); MIS i,xii (ADW); PV (De la Maza 1987), xii (ADW).

Arcas cypria (Geyer 1837). AHU iii; LCA ix (MZFC).

Atlides halesus (Cr. 1777). BDH i,xi,xii (López 1989).

Atlides gaumeri (Godm. 1901). AHU vi (MZFC); AJI xii (USNM); BDH i,xi,xii (López 1989); GUA (USNM); LCA vi (ADW).

Atlides polybe (L. 1763). BES iii (IMCyP, Abud 1987,1988); LCA ix,xi (MZFC).

Atlides carpasia (Hewit. 1868). ADJ (Rodríguez 1982), xii (CIB).

"Thecla" (umbratus group) **umbratus** (Geyer 1837). AHU x (MZFC); BDT xii; CHIS xii (ADW).

"Thecla" (ligurina group) **ligurina** (Hewit. 1874). BDT xii (ADW); LCA ix (MZFC).

Orcya bassania (Hewit. 1868). AJI xii (CMNH, Johnson 1990); EC iv (MZFC); PLM xi (MZFC).

Contrafacia imma (Prittwitz 1865). BDH i,xi,xii (López 1989).

Thereus oppia (Godm. & Sal. 1887). MIS xii (ADW).

Arawacus togarna (Hewit. 1867). El Potrero ix (CIB).

Arawacus sito (Boisd. 1836). AHU xi (MZFC); EBC x (CIB, Beutelspacher 1982); CHIS xii (ADW); LCA iv,vi,ix,xi (MZFC); MIS i,xii; PV xii (ADW), ix (Comstock & Vázquez 1961); TEN xii (LACM).

Arawacus jada (Hewit. 1867). AHU ii,iii,vi,viii,x (MZFC); BDH i,xi,xii (López 1989); Barranca de Oblatos ix (USNM); ELT iii (MZFC); GUA; Juchitlán ix (USNM); LDC (Godm. & Sal. 1878–1901); LCA iv,xi (MZFC); MIS i,xii (ADW); Ocotlán ix (USNM); PLM x,xi (MZFC); PV iii,xii (ADW); PV, 53 km S, on Hwy 200 i (LACM); Tecolotlán ix (USNM).

Rekoa meton (Cr. 1780). AHU iii (MZFC); BDT xii (ADW); LCA viii,xi (MZFC).

Rekoa palegon (Cr. 1780). AHU iii,vi (MZFC); AJI (Robbins 1991); BDT i (ADW); CHIS xii (ADW); GUA (Robbins 1991); LCA vi (ADW); MIS i; PV iv (ADW); PV, 34 km S i; RT at Hwy 200 i (LACM); ZEN vi (ADW).

Rekoa zebina (Hewit. 1869). AJI (Robbins 1991); BDT xii (ADW); BOL (Robbins 1991); BDH i,xi,xii (López 1989); BES ix (IMCyP, Abud 1987,1988); EBC viii (CIB); GUA (Robbins 1991); LDC (Robbins 1991); Mirador (Robbins 1991); MIS iii; PV xii (ADW).

Rekoa marius (Lucas 1857). AHU iii (MZFC); BDT xii (ADW); BOL (Godm. & Sal. 1878–1901); GUA (Robbins 1991); LCA iv,xi (MZFC), vi (ADW); MIS iii,xii (ADW).

Rekoa stagira (Hewit. 1867). LCA vi,xi (MZFC); PV xii (ADW).

Ocaria ocrisia (Hewit. 1868). AHU viii,x (MZFC); BDT xii; CHIS i (ADW); LCA ix,viii,xi (MZFC), vi (ADW); LDC (Godm. & Sal. 1878–1901); ZEN viii,xi (MZFC).

Chlorostrymon simaethis (Drury 1773). AJI xii (CMNH).

Chlorostrymon telea (Hewit. 1868). AHU viii (MZFC).

Cyanophrys amyntor (Cr. 1776). MIS i (ADW).

Cyanophrys herodotus (Fabr. 1793). AHU iii (MZFC); BDH i,xi,xii (López 1989); LCA vii (MZFC); MIS i,xii (ADW); PV vi (Kendall & McGuire 1984), i,xii (ADW), ix (Comstock & Vázquez 1961).

Cyanophrys miserabilis (Clench 1946). AHU iii,v (MZFC); AJI xii (Clench 1981); EBC i (CIB); GUA (USNM); LCA ix,xi (MZFC), vi (ADW).

Cyanophrys longula (Hewit. 1868). AHU iii (MZFC); BDH i,xi,xii (López 1989); ECLO III; Los Asoladeros del Tlacuache, EC v; PLM x (MZFC).

Callophrys xami (Reak. 1867). JAL (Clench 1981).

Callophrys spinetorum (Hewit. 1867). BOL (Godm. & Sal. 1878–1901, Shields 1965), vii (BMNH, Johnson 1985).

Panthiades bitias (Cr. 1777). EBC ix (Opler, pers. comm., 1993); LCA viii (MZFC); GUA (AMNH, Nicolay 1976).

Panthiades bathildis (Feld. & Feld. 1865). AHU iii (MZFC); AJI x,xii (CMNH; Nicolay 1976); BDH i,xi,xii (López 1989); BDT xii (ADW); LCA ii,ix,xi (MZFC); MIS i,xii; PV xii (ADW).

Oenomaus ortygnus (Cr. 1780). LCA iv (MZFC).

Parrhasius polibetes (Cr. 1782). LCA ix,xi (MZFC).
Parrhasius orgia (Hewit. 1867). BDH i (López 1989); EBC x (Beutelspacher 1982).
Parrhasius moctezuma Clench 1971. BDH i,xi,xii (López 1989); LCA ix,xi (MZFC).
Michaelus hecate (Godm. & Sal. 1887). GUA (USNM, Nicolay 1979); LCA v (MZFC), vi (ADW).
Michaelus vibidia (Hewit. 1869). GUA (Nicolay 1979); LCA vi (ADW), ix (MZFC).
Strymon melinus (Hübner 1813). AJI xii (CMNH); CHP x (LACM).
Strymon albata (Feld. & Feld. 1865). AHU viii (MZFC); BDT i,xii (ADW); EBC x (CIB, Beutelspacher 1982); LCA ii (MZFC); MIS i,iv,xii (ADW); PLM iii (MZFC); PV xii (ADW).
Strymon alea (Godm. & Sal. 1887). JAL (Clench 1966).
Strymon rufofusca (Hewit. 1877). AHU iii,viii (MZFC); EBC i–iii,xii (Beutelspacher 1982), iii,xii (CIB); ZEN ix (MZFC).
Strymon bebrycia (Hewit. 1868). AHU vi (MZFC); BDH ix,vi,viii (López 1989); EBC i,ii,xii (CIB); LCA ix (MZFC); MIS iii,xii (ADW).
Strymon bazochii (Godart 1824). AHU vi; Lagos de Moreno, 20 km N vi; PLM vi; ZEN vii (MZFC).
Strymon yojoa (Reak. 1867). AHU ii,vi (MZFC); EBC ii,x,xii (Beutelspacher 1982); CHP xii (CIB); GUA (USNM); LCA vi (ADW); xi (MZFC); MIS i,xii (ADW); PLM viii (MZFC); YEL ii (LACM).
Strymon cestri (Reak. 1867). AHU x, (MZFC); AJI xi,xii (CMNH); LCA xi (MZFC).
Strymon istapa (Reak. 1867). AHU iii,vi (MZFC); BDH i,xi,xii (López 1989); Barranca de Oblatos ix (USNM); BDT i,xii (ADW); CHIS xii (ADW); GUA vii (USNM); MIS i,iii,iv,xii; PV i,iii,iv,xii (ADW); YEL ii (LACM).
Strymon ziba (Hewit. 1868). LCA ix (MZFC).
Strymon megarus "complex" (Godart 1824). CHM iii (USNM); MIS i (ADW).
Lamprospilus collucia (Hewit. 1877). LCA ix (MZFC).
"***Thecla***" (***arza*** group) ***tarpa*** (Godm. & Sal. 1887). AHU iii (MZFC).
"***Thecla***" (***hesperitis*** group) ***hesperitis*** (Butl. & Druce 1872). LCA ix (MZFC).
"***Thecla***" (***hesperitis*** group) nr. ***hesperitis*** (Butl. & Druce 1872). BDT xii (ADW); LCA ix,xi (MZFC).
"***Thecla***" (***hesperitis*** group) ***ceromia*** (Hewit. 1877). BDT xii (ADW).
"***Thecla***" (***hesperitis*** group) ***sethon*** (Godm. & Sal. 1887). PLM xi (MZFC).
"***Thecla***" (***hesperitis*** group) ***guzanta*** (Schaus 1902). AHU vi; ECET iii; LCA xi; ECLO iii; ECPE iii; PLM xi (MZFC).
Electrostrymon sangala (Hewit. 1868). BDT xii; PV iii (ADW).
Electrostrymon canus (Druce 1907). AHU iii (MZFC).
Calycopis demonassa (Hewit. 1868). AHU iv; LCA vi (MZFC).
Calycopis clarina (Hewit. 1874). GUA (USNM); MIS xii (ADW).
Calycopis isobeon (Butl. & Druce 1872). AHU iii,iv,vi (MZFC); BDH i,xi,xii (López 1989); BDT i (ADW); EBC x (Beutelspacher 1982, CIB); CHIS xii; LCA vi (ADW), ix,xi (MZFC); MIS i,xii (ADW); PV ii (LACM), iii,xii (ADW); ZEN viii (MZFC).
Tmolus echion (L. 1767). AHU iv (MZFC); BDT xii (ADW); LCA vi (MZFC); MIS xii (ADW); ZEN viii (MZFC).
"***Thecla***" (***opalia*** group) ***phobe*** (Godm. & Sal. 1887). CHIS xii (ADW).
"***Thecla***" (***keila*** group) ***keila*** (Hewit. 1869). AHU viii (MZFC).
Aubergina paetus (Godm. & Sal. 1887). PLM x (MZFC).
"***Thecla***" (***mycon*** group) ***mycon*** (Godm. & Sal. 1887). AHU x,xi; LCA xi (MZFC).
"***Thecla***" (***tephraeus*** group) ***tephraeus*** (Geyer 1837). AHU iv,vi (MZFC); BDT xii (ADW); LCA v,vi (MZFC); PV xii (ADW).
Ministrymon leda (Edw. 1882). BDH vi–xii (López 1989); CHP ii,ix (USNM); Jalostotitlán viii (CIB).
Ministrymon clytie (Edw. 1877). AHU iii,x, (MZFC); CHP ix,xii (USNM); LCA vi (ADW), IX; ZEN xi (MZFC), vi (ADW).
Ministrymon phrutus (Geyer 1832). LCA ix; ZEN vi,ix (MZFC).
Ministrymon azia (Hewit. 1873). AHU iii,viii,x,xi; LCA vi (MZFC); LDC (Godm. & Sal. 1878–1901); MIS i,xii; PV xii (ADW); ZEN vi,ix,viii,xi (MZFC).

Ipidecla miadora Dyar 1916. BDH vii–xii (López 1989); LCA xi (MZFC).
"Thecla" (***upupa*** group) ***maeonis*** (Godm. & Sal. 1887). EC iv; PLM vi,viii (MZFC).
Brangas neora (Hewit. 1867). GUA (USNM); LCA ix,xi (MZFC).
Chalybs hassan (Stoll 1791). LCA ix,xi (MZFC).
Hypostrymon critola (Hewit. 1874). EBC x (CIB).
Erora nitetis (Godm. & Sal. 1887). PLM xi (MZFC).
Erora carla (Schaus 1902). BDT xii (ADW); LCA ix (MZFC); MIS xii (ADW).
Caerofethra lucagus (Godm. & Sal. 1887). ECLO iii (MZFC).
Brephidium exilis exilis (Boisd. 1852). BES i–xii (IMCyP, Abud 1987,1988); EBC v (Beutelspacher 1982); Cojumanatlán ix (USNM); PV ix (Comstock & Vázquez 1961), vii (LACM); ZEN vi (MZFC).
Leptotes cassius striata (Edw. 1877). AHU iii,iv,vi,viii–xi (MZFC); AJI v,vi,viii–xi (CMNH); BDT i,xii (ADW); EBC ii,vi,ix–xii (Beutelspacher 1982); CHIS i,xii (ADW); ELT iii (MZFC); LCA i,ii,v–xi; ECLO iii; EC iv (MZFC); MIS i,iii,iv,xii (ADW); PLM vi,x (MZFC); PV i,iii,iv,xii (ADW); PV, 60 km S i YEL ii (LACM); ZEN vi-ix,xi (MZFC).
Leptotes marina (Reak. 1868). ADJ (Rodríguez 1982), i–iii,v,x (CIB); AHU iii,v,vi,viii (MZFC); AJI iv–xii (CMNH); BDH xi,xii (López 1989); CHIS xii (ADW); LCA xi (MZFC); LDC (Godm. & Sal. 1878–1901); Ocotlán viii (USNM); PLM v,x; ZEN vi,vii (MZFC).
Zizula cyna cyna (Edw., 1881). AHU iii; AJI iv,x,xi (CMNH); ELT iii (MZFC); LCA viii; PLM iii (MZFC); PV iv (LACM), xii (ADW); PV, 30 km S, on Hwy 200 v (LACM); ZEN vii (MZFC).
Hemiargus ceraunus zachaeina (Butl. & Druce 1872). ADJ (Rodríguez 1982), ii,v,vi,x (CIB); AHU ii,iii,v,vi,viii–xi (MZFC); AJI iv,v,vii–xii (CMNH); ECAL iii (MZFC); BDH i–xii (López 1989); BDT i,xii (ADW); BOL (Godm. & Sal. 1878–1901); CHM (Rodríguez 1982); EBC v (Beutelspacher 1982); CHP ix (USNM); CHIS i,xii (ADW); Cocula IX; Cojumanatlán ix (USNM); GUA (USNM); LCA i,v–vii,xi; ECLO iii (MZFC); LDC (Godm. & Sal. 1878–1901); MIS i,iii,iv,xii (ADW), iv (LACM); Ocotlán viii (USNM); ECPE iii (MZFC); PV iv (LACM), i,iii,iv,xii (ADW); PV, 60 km S i (LACM); Tecolotlán ix (USNM); ZEN v–vii,ix,xi (MZFC).
Hemiargus isola isola (Reak. [1867]). AHU xi, (MZFC); AJI ix–xii (CMNH); ECAL iii (MZFC); BDH xi,xii (López 1989); BOL (Godm. & Sal. 1878–1901); BES ii,v,x,xi (IMCyP, Abud 1987,1988); CHP IX; Cocula ix (USNM); ECET iii (MZFC); GUA viii (CMNH); Ocotlán viii (USNM); ECPE iii; PLM v,vi,xi (MZFC).
Celastrina gozora (Boisd. 1870). AJI viii,ix,xi (CMNH); AHU iii,vi,x,xi (MZFC); BDH i,xi,xii (López 1989); BES i,ii,v,viii,xii (IMCyP, Abud 1987); LCA vi,xi; ECLO iii; EC iv (MZFC); Mazamitla x (SDNHM); PLM iii,vi,viii,xi (MZFC).
Everes comyntas (Godart [1824]). AHU iii,vi (MZFC); AJI vi,ix,x (CMNH); BDH i (López 1989); CHP iv (USNM); ECLO iii (MZFC); MIS xii; PV iii,iv (ADW); PV, 30 km S, on Hwy 200 iii,iv (LACM).
Icaricia acmon texana Goodpasture 1973. BES i,ii (IMCyP, Abud 1987,1988).

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GENERAL NOTES

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ESTABLISHMENT OF *PAPILIO DEMOLEUS* L. (PAPILIONIDAE) IN JAVA

Additional key words: distribution, Indonesia, Sunda Islands, Malay Archipelago.

Until the 1970s, *Papilio demoleus* L. was known from southern Asia, Australia and New Guinea, but not from most islands of the Malay Archipelago, except the Lesser Sunda Islands (Corbet & Pendlebury 1978). However, the species has expanded its range and become common in the Philippines (ssp. *libanius* Fruhstorfer from Taiwan) and Sumatra (ssp. *malayanus* Wallace from the Malay Peninsula) (Tsukada & Nishiyama 1980). In 1988 Kato (1989) collected a female *P. demoleus malayanus* in West Java, and reported it as the first record of the species in Java. Moonen (1991) pointed out that three earlier Java records existed for this species—two from East Java during the 1890s (race unclear, see Moonen 1991 for details), and one from West Java in 1914 (ssp. *malayanus*)—but he also mentioned that an established population of *P. demoleus* had never been found in Java.

However, to our knowledge, at least since 1990 *P. demoleus* has been rather common in West Java (at Ujung Kulon, Carita, Pelabuhan Ratu, Sukabumi, Cikampek and Garut). We also have observed this species in Central Java (at Kebumen, Kartasura and Surakarta)

FIGS. 1–2. *Papilio demoleus malayanus* collected in Java: **1**, male (Bogor, W. Java, 2 March 1991); **2**, female (Kediri, E. Java, 4 January 1992).

and East Java (at Ngawi, Nganjuk, Kediri and Ponorogo) from 1991 to 1994. Therefore, we consider the species has already become established and spread on the Island of Java. We have collected a number of Javanese specimens and deposited these in the Museum Zoologicum Bogoriense. The data for these specimens are as follows: WEST JAVA: ♂, Kebun Raya Bogor, 5 Sep 1990; ♀, Baranangsiang, Bogor, 25 Dec 1990; ♀, Kebun Raya Bogor, 24 Feb 1991 (em.); 2♀, Kebun Raya Bogor, 26 Feb 1991 (em.); 2♂ ♀, Pagilaran, Bogor, 2 Mar 1991; ♀, Cimanglid, Bogor, 26 Mar 1991 (em.); 2♀, Cimanglid, Bogor, 10 Apr 1991 (em.); ♂, Cimanglid, Bogor, 11 Apr 1991 (em.); ♂, Kebun Raya Bogor, 18 Apr 1991 (em.); ♀, Sukaluyu, Bogor, 5 Mar 1992; ♂, Bogor City, 21 Mar 1992; ♂, Curug Nangka, 13 February 1994; ♀, Pasir Mulya, Bogor, 7 March 1994. EAST JAVA: ♂ ♀, Wates, Kediri, 27 Mar 1992; ♀, Ngancar, Kediri, 4 Jan 1994; ♂, Ngawi, 26 Jan 1994. All the above specimens were identified as *P. demoleus malayanus* (Fig. 1–2). This suggests that the founder of the Javanese population invaded from the west, probably from Sumatra where the same race is now common (Tsukada & Nishiyama 1980). Kato's (1989) record may represent an early member of the present population.

Two males and six females from Bogor were bred from eggs or larvae found on *Citrus hystrix* DC., *C. aurantifolia* Swingle and *C. amblyocarpa* Ochse (Rutaceae). These species are commonly planted in home gardens in Java, and, as far as in West Java, the immatures of *P. demoleus* are frequently found on them. We have also seen a larva feeding on *C. grandis* Osbeck in Bogor. The Javanese population of *P. demoleus* is thus supported by cultivated *Citrus* spp. as in other Asian regions (e.g., Corbet & Pendlebury 1978), not by leguminous hosts as in Australia (Common & Waterhouse 1981). The aforementioned breeding yielded a number of pupal parasitoids, including *Brachymmeria* sp. and *Eulophidae* sp. (Hymenoptera).

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NOTES ON THE NATURAL HISTORY OF *DOXOCOPA EXCELSA* (NYMPHALIDAE: APATURINAE) IN TURRIALBA, COSTA RICA

Additional key words: *Astraptes, Celtis,* phenology, rarity.

Butterflies of the genus *Doxocopa* Hübner (Apaturinae) are among the least well-known nymphalids of the neotropics. DeVries (1987) records nine species of *Doxocopa* from Costa Rica, but reports hostplant records and partial descriptions of the early stages for only three. A detailed description of the life history has been presented for only one species in the genus, *D. laure* Drury (Muller 1886), and the larva and pupa of *D. cyane burmeisteri* Godman and Salvin were figured by Schreiter (1943).

Doxocopa excelsa (Gillott) is one of the rarest species of *Doxocopa* in Central America; it is known only from El Líbano and Turrialba in Costa Rica, and from Chontales in Nicaragua (DeVries 1987, pers. comm.). The hostplant and early stages of this species have not been recorded previously, although limited life history information was obtained by Andrew King. During his residence in Turrialba, King observed *D. excelsa* only during June and July (also see DeVries 1987) and concluded that it was strongly seasonal in its occurrence.

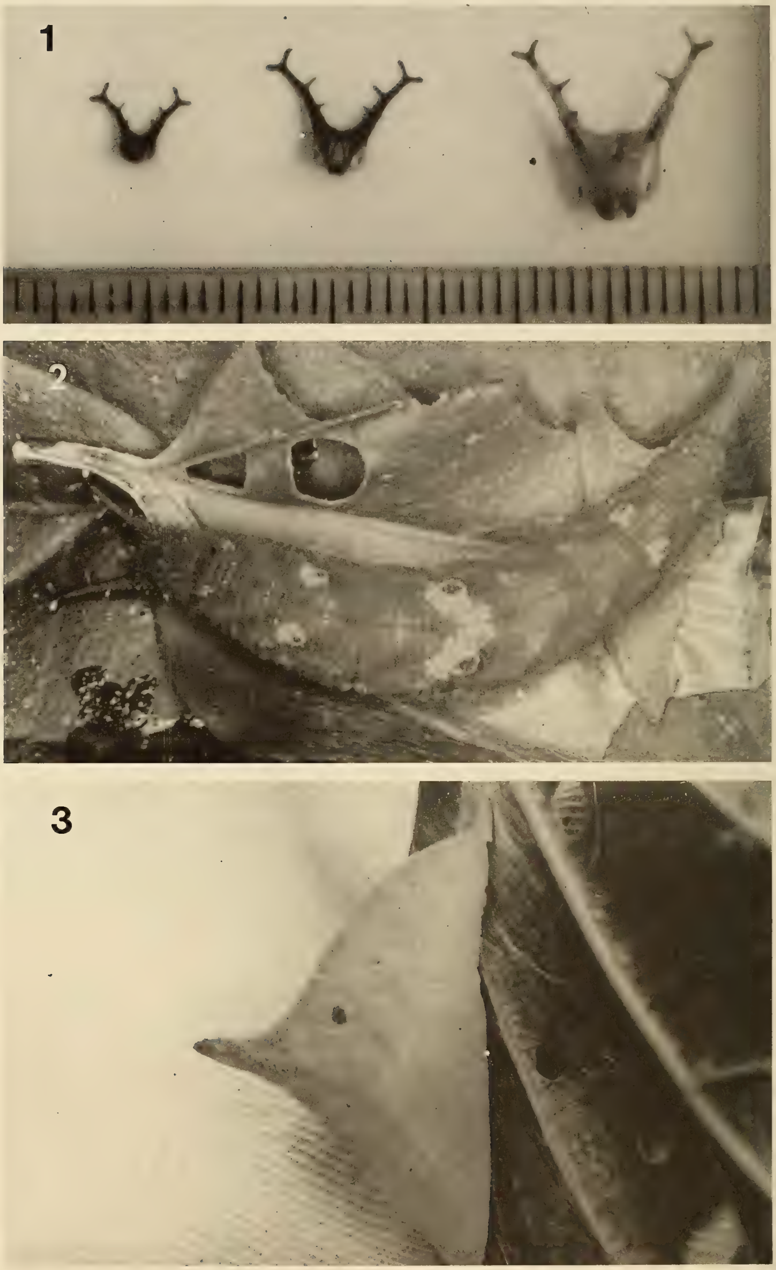
This paper reports the results of studies on *Doxocopa excelsa* conducted at Turrialba, Costa Rica, by the author, and presents descriptions of three larval instars and the pupa. Brief observations are presented on larval behavior, as well as on the biology and ecology of the hostplant and possible relationships to the ecology and population dynamics of the butterfly.

Turrialba is located at 600 m above mean sea level on the Central Volcanic Cordillera of Costa Rica. Mean annual temperature is 22°C and mean annual rainfall 2500 mm. The study was conducted in Los Espaveles, a 20 ha forest fragment located in the canyon of the Reventazón River supporting disturbed primary and secondary vegetation (Salcedo 1986).

Descriptions of the early stages are composite, based on four individuals, three of which were successfully reared to adults. The first larva was found on 7 May 1992. It was 12 mm long and passed through three instars (presumably 3rd, 4th, and 5th) before pupating. The second larva, that apparently had recently moulted into what proved to be its final (5th) instar, was found on 7 September 1993. A third larva was found on 20 October 1993 in what is assumed to be the fourth instar. This larva died soon after being found, possibly from careless handling in the field. The fourth larva was found in its final instar on 6 June 1994.

Third instar. Head capsule 1.7 mm in width, with two stout horns, each approximately 3 mm in length (Fig. 1). Horns with forked tips and two slender, inward pointing branches. Face and front part of horns shiny black; three rather indistinct white marks on the lower face; circular whitish patch around stemmata. Rear part of head and horns shiny dark tan. Body uniform green with rough, warty texture. Two transverse, raised, bright yellow oblong patches on dorsum of segment A4. Tail bifid with the two parts held tightly together as in larvae of other *Doxocopa.* Near end of stadium, two yellow dots increasingly evident on dorsum of each segment, except on segments A3 and A4; particularly conspicuous on segments A2, A5, and A7 at distal edge of segment. Segment A3 with dots at caudal edge of segment adjacent to the yellow oblong patches of segment A4; segment A4 with dots between yellow oblong patches. The third instar moulted four days after its discovery. Total length including bifid tail 15 mm.

Fourth instar. Head capsule width 2.7 mm; horns 4 mm long, forked and branched as in third instar (Fig. 1). Head and horns pale greenish tan posteriorly; sides of the head green, with small white dots. Most of face and front of horns shiny black, frons and clypeus shiny pale grey. Frons lined in black with shiny pale grey triangle covering the adfrontal area on each side, visible as translucent areas in Fig. 1. Inner vertices of triangles connate



FIGS. 1–3. Head capsule, larva, and pupa of *Doxocopa excelsa* from Turrialba, Costa Rica. **1**: Head capsules of third, fourth, and fifth instar larvae (from left to right); scale in mm. **2**: Final (fifth) instar larva on its hostplant, *Celtis* cf. *iguanaeus*. Larva exhibits typical

at epicranial suture. Body green, markings as described for third instar, but pale yellow; covered with small pale yellow dots evident upon close examination. Markings on segments A3 and A4 as in fourth instar, but yellow; dots on dorsum greatly enlarged on segments A2 and A7, visible but indistinct on other segments. Spiracles surrounded by small pale yellow dot. Total length including bifid tail approximately 34 mm. The fourth instar lasted only four days.

Fifth instar. Head capsule width 4.8 mm; forked horns 6 mm long (Fig. 1). Each horn with single, slender, inward-pointing branch at its middle, with several smaller protuberances below. Body color green, with minute greenish white dots. Series of indistinct dark green to purplish diagonal bands, each starting at lower center of segment and terminating at caudal edge of following segment; dark bluish green dorsal midline. Markings similar to those in previous instar evident on distal edges of segments A2, A4 and A7, in form of an irregular greenish white blotch with a purplish circle in the center of each (Fig. 2). Blotches on A4 largest, those on A7 smallest. Small greenish white dot opposite each blotch on preceding segment (Fig. 2). Total length 47 mm. The fifth instar lasted 8–10 days.

Pupa. Approximately 30 mm long, similar in shape to that of *Doxocopa clothilda* (DeVries 1987:fig. 21), but with segment A5 produced into a short spike (Fig. 3). Same color green as larva, with faint dark green or purplish diagonal stripes, a prominent purplish dot on segment A6, and a smaller dot of the same color on segment T2 (present in first individual reared). Abdominal spike and keel purplish. Cremaster green below, black at pupal attachment to substrate. The pupae wriggled vigorously when molested. The pupal stage lasted 10–12 days.

The first individual (male) emerged on 3 June 1992; the second (female) on 27 September 1993; and the third (female) on 29 June 1994. Voucher specimens (one male, one female, one pupal case, and the head capsules illustrated in Fig. 1) are deposited in the Museo Nacional in San José, Costa Rica.

All larvae were found and reared on shoots of the same individual of the liana *Celtis* cf. *iguanaeus* (Jacq.) Sarg. (Ulmaceae). A voucher specimen of the hostplant is deposited in the Museo Nacional. This large *Celtis* has its crown in the canopy of a secondary forest (approximately 20 years old) that has developed on an abandoned coffee plantation on the upper terrace of the Los Espaveles forest. The shoots upon which larvae were found were about 0.5–3.0 m tall and were produced from the 5–10 cm diameter lower shoots and root system of the plant. *Celtis* is found more commonly at forest edges than within the forest at the Los Espaveles site, though it was formerly abundant in other secondary forests on the CATIE estate (Martín Artavia, pers. comm.). It appears to be relatively light-demanding. In the forest understory, new basal leaf shoots produced in May, June, and July mostly die back by September; I have not observed flowering or fruiting. In contrast, forest-edge plants grow vegetatively, flower, and fruit unimpeded.

As is evident in Fig. 2, larvae of *D. excelsa* are well camouflaged on their *Celtis* host. The first individual was noticed only because of the dark color of the rear of the head capsule in the third instar. Larvae rest on the upper surfaces of leaves with the face flat against the leaf surface (Fig. 2; see also DeVries 1987:fig. 21 for other *Doxocopa* spp. and for identical behavior in larvae of British *Apatura iris*, Thomas & Lewington [1991]). Larvae usually rest towards the leaf tip where they make a silken pad that raises the leaf surface towards the larva, but does not cover it. As the dark color of the rear of the head capsule becomes green in later instars, the camouflage is complete. The white and purplish markings on the body appear to mimic those on mature *Celtis* leaves dotted with epiphylls (Fig. 2).

Reasons for the apparent scarcity of *Doxocopa excelsa* are unclear. The availability of

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cryptic resting position with face (at left of photo) flat against leaf surface. Length of fully extended larva 47 mm. **3**: Pupa suspended (cremaster at top) from leaf of hostplant. Pupal length 30 mm.

hostplants would not appear to be limiting. The Turrialba hostplant is widely distributed throughout tropical and subtropical America (see e.g., Croat 1978, Standley 1937). *Celtis* is also the hostplant of *D. cyane* Latreille, which is the most common *Doxocopa* in Costa Rica (DeVries 1987). Competition for the hostplant does not appear to be important. The individual *Celtis* plant which yielded the four larvae has been repeatedly searched since June 1992, and no other larvae of *Doxocopa* spp. have been found, although *D. pavon* Latreille and *D. cyane* also appear to be resident at Turrialba (pers. obs.). The Turrialba *Celtis* is also the hostplant of an *Astraptes* sp. (Hesperiidae: Pyrginae; pers. obs.), whose larvae are found much more frequently than those of *D. excelsa*. However, this *Astraptes* does not seem to represent a serious competitor. During the period of observation of this study, larvae of the hesperiid were never frequent enough to reduce the available foliage significantly, most disappearing while still in first or second instars after inflicting very little damage on the host.

The seasonality of *D. excelsa* at Turrialba (King, cited in DeVries 1987) is as difficult to explain as the insect's scarcity. It is likely, however, that more thorough studies may reveal large population fluctuations, but not seasonally linked presence and absence. The emergence of the male and the second female during the present study coincided with the period predicted from King's observations. On the other hand, the first female reared extends the flight period to September, and the fourth instar larva found in October, had it survived, would have emerged as an adult in November. The only individuals I have seen in nature also unequivocally extend the flight period: a male at a sunny forest edge recorded in the first week of August 1992 and a female seen in the forest understory on 8 January 1994 at 1100 h, apparently searching for hostplants.

Fluctuations in the abundance of this butterfly may correspond with the annual flushing of tender young shoots of the hostplant. Detailed phenological observations of *Celtis* are required to confirm that flushing is annual, but if young larvae are only able to consume such shoots, this would represent an important limiting factor (cf. Aide & Londoño 1989). As far as adult resources are concerned, the *Mikania* (Compositae) vine mentioned by DeVries (1987) flowers in discrete periods several times a year (pers. obs.), not only during June and July when adult butterflies were observed flying by King.

I am indebted to Phil DeVries for his book, which rekindled my childhood love of butterflies, and for encouragement and comments on an earlier draft of this note. Tim Friedlander drew my attention to the paper by Schreiter.

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THE INTRODUCTION AND SPREAD OF *CHLOROCLYSTIS RECTANGULATA* (L.) (GEOMETRIDAE), AND ITS FIRST REPORTED OCCURRENCES IN THE UNITED STATES

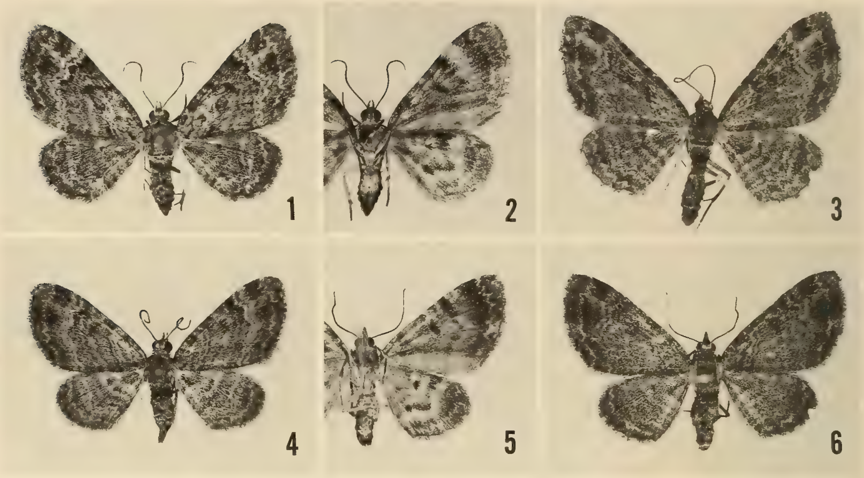
Additional key words: introduced moth, apple, pear, dispersal rate.

The palearctic fruit-tree pest, *Chloroclystis rectangulata* (L.), was first reported from North America based on Nova Scotian specimens collected at three widely separated sites in 1970 (Ferguson 1972), and the species is now generally distributed and common in that province. Between 8–18 July 1994 the senior author was able to verify the continued presence and abundance of *C. rectangulata* in Nova Scotia, where it was present at every collecting site in Yarmouth, Annapolis, Pictou, and Colchester counties. The largest numbers encountered came to light in shrubby meadowland and mixed woodland at a site southwest of Granville Ferry, Annapolis County. It apparently spread rapidly to neighboring provinces and was first reported from western Newfoundland at Stephenville in 1976 (Morris 1980:223), and from New Brunswick at Sussex, Kings County in 1978 (Neil 1980). It subsequently was collected at Doyles, southwestern Newfoundland in 1983, 1987, and 1988 by the late L. P. Grey (specimens at American Museum of Natural History), and at Pasadena, on Deer Lake, Newfoundland (reared from apple in 1982, 1983, and 1989); was found in various localities in New Brunswick in 1977, 1985, and 1987; and at Douglastown on the Gaspé Peninsula, Quebec (reared from apple, 1989) (J. D. Lafontaine, pers. comm.). It was collected at Enfield [Penobscot County], Maine every year from 1982 to 1987 by L. P. Grey (AMNH). Ten specimens were collected on Mount Desert Island, Hancock County, Maine in 1989 by G. J. Balogh, who deposited five of them in the Canadian National Collection; and one was taken at Lamoine [Hancock County], Maine in 1991 (AMNH). Paul Grey's specimens from Enfield, Maine, 15–18 July 1982, deposited in the American Museum of Natural History (AMNH), are evidently the first records for the United States but were not reported.

Chloroclystis rectangulata recently appeared in New Hampshire and Massachusetts, having reached southern Massachusetts seven years after its first known occurrence in northeastern Maine and four years before being found in New Hampshire. However, considering the relatively few observers of small moths in Northern New England, it easily could have been present but undetected years earlier. Eight specimens were collected by the junior author at widely separated localities in four counties of Massachusetts, as follows: Truro, Barnstable County, 8 July 1989; South Dartmouth (Lloyd Center), Bristol County, 7 July 1992, 19 June 1994, 26 June 1994; Minot Road, Westminster, Worcester County, 26 June 1993; Plymouth, Plymouth County, 24 June 1993 (Fig. 3), 16 June 1994 (Figs. 1–2), 23 June 1994. One specimen was collected at Whitefield, Coos County, New Hampshire on 6 July 1993, and five more were taken at the same locality on 25 and 29 June, and on 5 and 12 July 1994 (W. J. Kiel, in litt.).

Although these records suggest that there is now a continuous distribution from eastern Canada to southern Massachusetts, major gaps remain through southern Maine and southern New Hampshire. In the absence of data from these intervening regions, it is not certain whether the Massachusetts specimens indicate a continuous range extension from Nova Scotia or a separate introduction. It should be noted that the distance from Hancock County, Maine to Whitefield, New Hampshire is nearly equal to the distance from the same point in Maine to the Massachusetts-New Hampshire border, suggesting that if the species could spread to northwestern New Hampshire, especially through or around a region of high mountains, it could just as easily have reached Massachusetts. We think it likely that the present distribution is a continuous one, and that the apparent gaps are the result of inadequate sampling.

Alternatively, this species might have been assisted by transport with agricultural products, as a hitchhiker in vehicles, or by a natural, wind-assisted, long-range dispersal event,

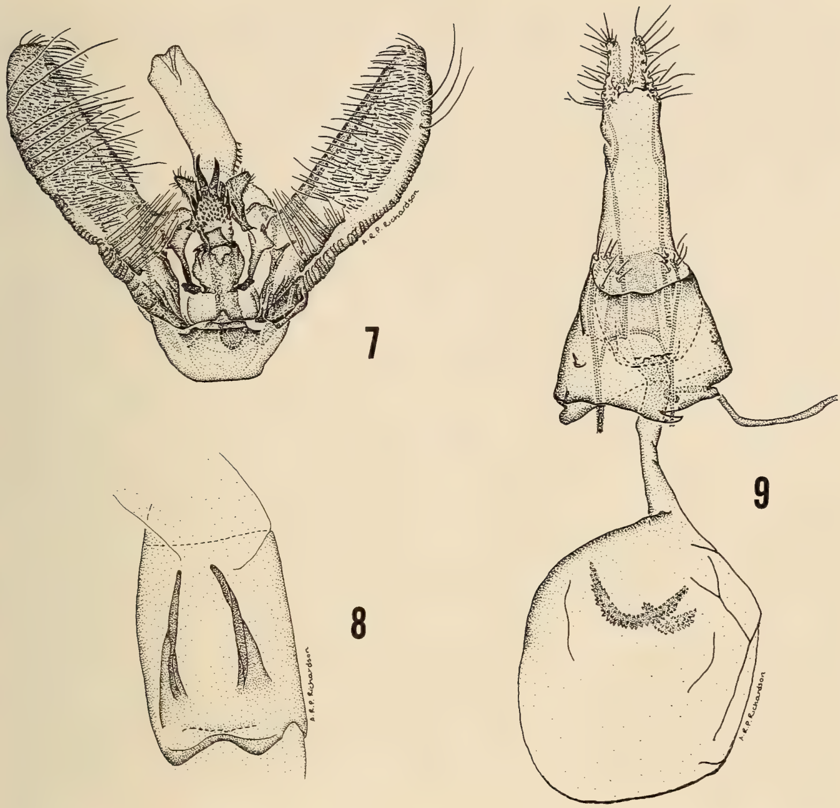


FIGS. 1–6. *Chloroclystis rectangulata* (all are females, magnification 2x). **1**, Plymouth, Massachusetts, 16 June 1994. **2**, same specimen, underside. **3**, dark form, Plymouth, Massachusetts, 24 June 1993. **4**, Granville Ferry, Annapolis Co., Nova Scotia, 8 July 1994. **5**, same specimen, underside. **6**, dark form, same data as Fig. 4.

although such explanations are probably not needed to account for its presence in New Hampshire and Massachusetts. The most easily transported stage would be the overwintering eggs on nursery stock, probably explaining how the species reached this continent. At this rate of spread, about 756 km from Nova Scotia to southern Massachusetts in 19 years, or 40 km/yr, *C. rectangulata* would be expected to occupy nearly all suitable habitat across the continent from a single East Coast introduction site in about 100 years; but because of an expanding West Coast population, and possibly other random dispersal events facilitated by man, the time required is likely to be less. This rate of spread (40 km/yr) is not unusual for introduced species (Ferguson, unpubl. data).

Remarkably, *C. rectangulata* appears to have been introduced almost simultaneously on the Atlantic and Pacific coasts of Canada, and is spreading outward from both sites. The Canadian National Collection contains one specimen from Victoria, British Columbia, collected in 1968, which was two years earlier than the first-reported records from Nova Scotia; and the senior author recently verified the identification of four specimens from Whatcom County, Washington. Three of these were reared from larvae on apple, and one from an unidentified tree. The species is therefore following an unexplained pattern of dual introductions noted for several other species of Lepidoptera e.g., *Thymelicus lineola* (Ochs.) (Hesperiidae), *Operophtera brumata* (L.) (Geometridae), *Leucoma salicis* (L.) (Lymantriidae), *Apamea ophiogramma)* (Esp.) (Noctuidae) and *Caradrina morpheus* (Hufn.) (Noctuidae).

Ferguson (1972) remarked upon the green wing markings and the genitalic features by which this species may be distinguished but provided no illustrations. Figs. 1–6 in the present paper show adults from Nova Scotia and Massachusetts, and Figs. 7–9 illustrate the genitalia of male and female specimens from Nova Scotia. Apart from the scattered bright-green scales on the otherwise mostly dark gray-brown uppersurfaces, the heavy dark markings on the undersurfaces of both wings distinguish *C. rectangulata* from most or all North American species of *Eupithecia*. The green scales may be lost, faded or discolored in poor specimens, although the green pigment appears to be of a type more resistant to fading than most. The spinose tip of the aedeagus, with a terminal pair of large, forcepslike spines, is particularly conspicuous and diagnostic in the male genitalia;



FIGS. 7–9. Genitalia of *Chloroclystis rectangulata*. **7**, ♂, Middle River, Victoria Co., Nova Scotia, 27 July 1970 (aedeagus in place). **8**, same specimen, 8th sternum, **9**, ♀, Baddeck Bridge, Victoria Co., Nova Scotia, 29 July 1970.

and also the weak triangular uncus is overshadowed by a very strong anal tube. In the female, the two lunate or crescentic spinulose signa, one on each side of the corpus bursae, serve to separate *C. rectangulata* from all North American members of the tribe Eupitheciini.

The life history was described by Barrett (1904:149–152), whose ten volume work is still one of the best sources of information on British Lepidoptera. The larvae feed in spring on blossoms of apple and pear, drawing the petals together and feeding within. The adults fly in June and July, and the eggs overwinter. The mature larva is short, stout, pale yellowish green, and translucent. The dorsal line is variable in color and intensity from rusty red to dark green, but may be indistinct or wanting. The spiracular (lateral) line is darker than the ground color, and the segmental divisions reddish. Younger larvae are darker, with the dorsal stripe broad, distinct, and rusty red.

Further details on the biology of *C. rectangulata* may be found in a paper by Clausen (1945), who gave references to other papers that will serve to supplement the few references provided by Ferguson (1972). The species is univoltine, and in south-central Europe the adults fly from about 29 May to late June; in Denmark they fly from mid-June to late July (Skou 1986:199), dates that are comparable to those for the Atlantic Provinces (3–29 July) and New England (16 June to 30 July). The eggs are deposited in

groups of 1–11 in crevices, fissures or injuries in the bark of twigs, branches or trunk, or under bud scales, with a preference being shown for twigs or smaller branches of 1–4 cm diameter. The eggs match the color of the bark and are not easily seen. The larvae develop within the eggs the same season and become visible through the shell 12–15 days after oviposition. However, they hibernate within the egg and do not hatch until the following spring. The eggs studied by Clausen hatched in March, and in the laboratory the larvae matured in 19–25 days on a night-day temperature cycle of 12–20°C. Outdoors under natural conditions the earliest larvae were found on 31 March and matured in 25–30 days. A forced second brood was evidently produced in the laboratory, and these larvae matured in 22–23 days. The pupal stage lasted 18–21 days under laboratory conditions.

The larvae reared by Clausen (1945) showed a definite preference for the flowers of cultivated apple and pear, feeding especially on the anthers. No attempt was made to rear them on leaves only. Those fed on pear flowers grew slightly more rapidly than those on apple. Although larvae were plentiful on pear and apple, none were found on the flowers of quince or the available varieties of plum, apricot, or cherry. Larvae that Clausen raised on those plants appeared to develop with difficulty and perished in large numbers, although in the literature there are references to *C. rectangulata* feeding on species of *Prunus, Crataegus,* and on quince (*Cydonia oblonga* Mill.). Most of the North American specimens were collected in or at the edges of mixed, natural woodland, not in the vicinity of orchards, and these habitats suggest that the species is thriving on native Rosaceae. Possible food plants in Nova Scotia include three native species of *Prunus* and several species of *Crataegus,* as well as cultivated or escaped pear or apple at some sites. It is not known whether native species of *Amelanchier, Rosa, Aronia, Sorbus,* or *Rubus* (Rosaceae) might serve as hosts.

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FIRE ANT PREDATION ON MONARCH LARVAE (NYMPHALIDAE: DANAINAE) IN A CENTRAL TEXAS PRAIRIE

Additional key words: milkweed, population dynamics, *Danaus plexippus, Asclepias oenotheroides, Solenopsis invicta.*

Little quantitative data concerning the means by which the monarch butterfly (*Danaus plexippus* L.) repopulates eastern North America exist. Our qualitative understanding of this process is essentially this: large monarch populations migrate southward from major breeding grounds located between the Rocky Mountains and the Atlantic Ocean north of ca. latitude 40°N at the end of summer (Urquhart 1987). Some fraction of these butterflies reach the overwintering grounds in central Mexico around the beginning of November (Calvert & Brower 1986). Due to predation, starvation, and desiccation at the overwintering sites, an even smaller number remigrate in the spring to the southern United States and presumably northern Mexico where they lay eggs on newly sprouted asclepiads to form the first spring generation (Malcolm et al. 1993). Here the population decline prevalent during late fall and winter reverses itself, and monarchs begin to increase in number. The monarch population is thought to build during each subsequent summer generation with major increases occurring at the end of summer in the northern breeding grounds. Basic factors such as the phenology and size of the migration, yearly variations in population size, and the pathway of travel from breeding to overwintering grounds and return are poorly understood.

I began the study reported here to determine the phenology of host plant use by monarch butterflies on a previously uninvestigated prairie milkweed (*Asclepias oenotheroides* Cham. & Schlecht., Asclepiadaceae), the distribution of which is southern—largely confined to Texas, Mexico, and Central America (Woodson 1954). My goal was to estimate reproductive success by examining the number of larvae reared successfully in a dense milkweed field in south-central Texas. The study was never completed because no larvae completed their development on this species. Fire ants (*Solenopsis invicta* Buren, Formicidae) appeared to consume all monarch larvae and eggs.

During the spring of 1995, I monitored a field of *A. oenotheroides* for the presence of monarch eggs and larvae at the Baptist Children's Ranch, located in the Blackland Prairies approximately 10 km southeast of Luling, Texas. The 0.99 ha pasture was visited 5 times between 29 March and 8 May, an average of every 9.75 days (Table 1). This 41-day period extended from the time when faded monarchs returning from Mexico were widely reported to the Texas Monarch Watch hotline (an 800 number service where information about the presence and abundance of monarchs in Texas and Oklahoma is exchanged) until none was being reported in central Texas. *Asclepias oenotheroides* stem densities were determined by the point-centered quarter method (Cottam & Curtis 1953). Stations were positioned every 10 m along two transects that ran perpendicular to each other through the center of the field. Egg and larval densities were determined by dividing the product of host plant stem density and the number of eggs or larvae by the number of stems examined.

Monarch egg and larval densities and *A. oenotheroides* stem density are shown in Table 1. *Asclepias oenotheroides* density started at about 1000 stems/ha, rose to nearly 4000 stems/ha, and stabilized at about 2600 stems/ha. The high density recorded on 7 April included many seedlings. The estimated number of eggs started at 508/ha on 29 March, peaked at 1243/ha on 7 April as the main group of returning migrants migrated through, and fell off as the migrants left the area. With the exception of the first count on 29 March, the number of adults observed during the count period corresponds well with the number of eggs counted (Table 1). The low adult number on 29 March is likely due to unseasonably cold weather that occured on that date.

With appropriate delays for time to develop, these eggs were expected to hatch and

TABLE 1. Estimated densities of *Asclepias oenotheroides* plant stems, *Danaus plexippus* eggs, larvae and adults in a 0.99 ha pasture near Luling, Texas. Total adults refers to the number of monarchs observed in the field during the ca. 2 hour period when data were taken.

Date	Total eggs	Egg density (eggs/ha)	Total larvae	Larval density (1st instars/ha)	Larval density (later instars/ha)	Stem density (stems/ha)	Stem height	Total adults
29 March	33	510	2	31	0	1047	5.87	1
7 April	20	1243	1	62	0	3729	7.78	23
15 April	5	206	0	0	0	2638	10.76	1
26 April	2	53	0	0	0	2569	10.74	0
8 May	1	47	0	0	0	2619	12.40	0

larvae were expected to proceed from instar to instar with fewer numbers in each subsequent stadium due to predation (Malcolm et al. 1987). However, no second or later instars were ever observed on any of the plant stems sampled.

Fire ants arrived in Mobile, Alabama from Brazil during the 1920s (Drees & Vinson 1993). Now, 70 years later, they have spread through much of the southern United States from North Carolina to Texas, an area where monarchs returning from Mexico are expected to lay eggs that will become the first spring generation (Malcolm et al. 1993). Fire ants are especially prolific on Texas prairies where their colonies are polygyne (multiply queened) (Porter et al. 1991) and may reach densities of 2000 mounds/ha (Drees & Vinson 1993). Fire ants specialize on arthropods (Porter & Savignano 1990) and have a reputation as voracious predators, even on vertebrates as large as cotton rats. Numerous anecdotal and published accounts document declines in arthropod populations as diverse as lone star ticks, chiggers, and cotton flea hoppers that occurred after the arrival of fire ants (Killion & Vinson 1995). In the vicinity of Austin, Texas, the abundance of lepidopterans has fallen to 50% of pre-fire ant levels (Durden, pers. comm.). Species most affected are those that feed near the ground on herbs or grasses. Durden argues that the decline in herb- and grass-feeding lepidopterans is due to fire ant predation.

On April 7, using the same stations employed by the point-centered quarter method to estimate host stem density, fire ant mound density was estimated to be 1011 mounds/ha. Occasionally stems of *A. oenotheroides* were found growing up through the mounds.

Fire ant presence on *A. oenotheroides* also was noted during the 41-day period. Approximately 4% of host plant stems examined for eggs or larvae had fire ants patrolling stems or leaves. Only a few spiders and no other predators were observed. On 29 March, a first instar larva was observed being attacked by fire ants on its host leaf. This incident is the only direct evidence that fire ants preyed upon monarchs during the study period. Fire ants were never observed in the process of removing or attacking eggs. There remains the possibility that other organisms or abiotic factors are responsible for the high rates of mortality observed. Nonetheless the overwhelming presence of fire ants in the field and their reputation as voracious predators suggests that they are the major factor in the failure of the monarchs to mature.

The location and distribution of prairies in the midwest with respect to those in Texas suggests that monarchs that breed on central Texas prairies and plains are the progenitors of monarchs that will breed on the prairies of Oklahoma, Kansas, Nebraska and further north (Malcolm et al. 1993). If the devastation of the population of monarchs oviposited on *A. oenotheroides* near Luling, Texas is indicative of what is occurring on *A. oenotheroides* located elsewhere and on other milkweed species used by monarchs, the first spring generation reared within the fire ant zone must make only a small contribution to the monarch recolonization of North America. No evidence exists as yet for similar effects in areas east of Texas where fire ants are also abundant, but eastern fire ants colonies are mostly monogyne (single-queened) and are not as dense as in Texas (Porter et al. 1991). Strong selection pressure may presently be in operation for monarchs returning from

Mexico to avoid areas of intense fire ant infestation and oviposit in fire ant-free areas to the north or west of the fire ant zone.

To my knowledge, this is the first empirical study that strongly implicates the imported fire ant in a negative impact on the population of the monarch butterfly.

This note has benefited greatly from discussions with Orley Taylor, Brian Hurt, Lincoln Brower, Leeanne Tennant and Alicia Nelson. I thank Alicia Nelson, Brian Hurt and Pat Hartigan for helping to collect the data. The manuscript was improved by the helpful comments of Sue Borkin and Lincoln Brower. I also thank James McWhorter and the staff of the Baptist Children's Home at Luling, Texas for their permission to conduct the study. The study was partially funded by the Texas Parks and Wildlife Non-Game Program, the Margaret Cullinan Wray Trust, and the Susan Vaughan Foundation.

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BOOK REVIEWS

THE BUTTERFLIES OF BRITAIN AND IRELAND, by Jeremy Thomas and Richard Lewington. 1991. Dorling Kindersley, London; published in association with The National Trust. 224 pp., 68 color plates, with distribution maps, life history charts, and halftone figures in the text. Hard cover, 25 × 25 cm, dustjacket, ISBN 0-86318-591-6. £16.99 (about $27 US).

Of all the world's lepidopteran faunas, those of the British Isles are known with unparalleled completeness, both as an historical and a biological record. For generations, throughout the Victorian era, and for much of the present century, collecting butterflies and moths (and, less commonly, other insect groups) was an accepted and widely encouraged avenue to an appreciation of the natural world. While many left behind their nets and store boxes with their childhood, a general level of interest and awareness often survived, and among those whose life continued into professional entomology, perhaps with staphylinids, pteromalids or mirids, many will admit to a transient phase of butterfly and moth hunting. This phenomenon is not, of course, an exclusively British peculiarity, but only there has an interest in these insects become something of a national institution. One may form the impression that a substantial part of the Anglican clergy, for a century or so, collected Lepidoptera when not engaged in more official pastoral duties, and when this reviewer went to a boarding school in Berkshire, at the age of ten, it seemed entirely natural that each pupil was expected to spend his free time in watching birds, pressing plants, or in the pursuit and rearing of butterflies and moths.

This venerable history of collecting was underpinned by, and reflected in a corresponding wealth of published books and local lists, from the first account to appear in Britain compiled by Thomas Mouffet (1634), which included often recognizable woodcuts of British Lepidoptera and other insects, with a few exotic "rarities." In the sequence that followed are the celebrated eighteenth century works: Benjamin Wilkes' *English Butterflies and Moths* (1749) and *The Aurelian* of Moses Harris (1766) and, in the flowering of Victorian passion for natural history, a spate of popular works, some well known and many now regarded as curiosities of the period. A few outstanding landmarks among more recent works are the finely illustrated eleven volumes of Charles Barrett's *The Lepidoptera of the British Islands* (1893–1907) and Richard South's works on British butterflies and moths, first published in the opening decade of this century, the latter acting as quasi-biblical texts for collectors young and old, for many years. To lepidopterists of this reviewer's generation, the seemingly unsurpassable illustrations of F. W. Frohawk could be admired only by the fortunate few with relatives sufficiently affluent to provide the "Complete Book" (1934), or even his two-volume folio work on the butterflies.

How much simpler and more satisfactory life would have been to a nascent entomologist, in 1945, had the book by Jeremy Thomas and Richard Lewington been available then! As the faunas in the British Isles (and in many parts of Europe) have dwindled in recent decades, the rate of books describing them has accelerated, and the past thirty years has seen over twenty new titles, but in this reviewer's estimation the account by Thomas and Lewington, in quality and balance of text, and artistry of illustration, is the finest account of British and Irish butterflies and their life histories, though appearing at a time when so many species are more likely to be enjoyed vicariously through its pages than seen in the field.

For many years the "British List" of butterflies stood at 68 species, including residents, a few occasional to very rare but well documented migrants, with the long extinct Large Copper (*Lycaena dispar dispar*) and Mazarine Blue (*Cyaniris semiargus*), the Black-veined White (*Aporia crataegi*) which disappeared early this century, and native populations of the Large Blue (*Maculinea arion*), last seen in 1979. Only one has been added in recent times: Berger's Clouded Yellow (*Colias alfacariensis*), distinguished in 1945 from another generally rare visitor, *C. hyale*. Of these, Jeremy Thomas has provided a succinct, lively and informative text, noting the present status of each with clear distribution maps, all too often tracing a species' decline in recent decades and, where possible, including the reasons for the sometimes precipitous range reduction: the Large Tortoiseshell (*Nymphalis polychloros*) now perhaps extinct as a resident, or the Chequered Skipper (*Carterocephalus palaemon*) now restricted to a few western Scottish colonies, and so on.

Any reader who knew the British butterflies in the 1950s and before will have memories of rich localities, of pastures, woods and downland from which once common species have long vanished, even if the land seems superficially to have survived. This book misses no opportunity for optimism, however: a few expanding ranges, of the Essex Skipper (*Thymelicus lineola*), the Speckled Wood (*Pararge aegeria*), and perhaps the White Admiral (*Ladoga camilla*), are recorded, together with current conservation efforts to keep now highly restricted and threatened species on the British list. To read this book in conjunction with South or Frohawk reveals the general and rapid decline of a fauna, for long relatively stable, for which the blame lies almost entirely with habitat change and degradation, in their richly varied aspects.

The illustrations, by Richard Lewington, have never, in my view, been surpassed. Each butterfly is shown by an upperside (of both sexes where appreciably dimorphic) in "set" position, and by an underside in "perching" pose. British lepidopterists have for long paid much attention to aberrations, and many very remarkable examples of these variants are shown. Other figures, illustrating the butterflies at rest or nectaring are particularly striking through Lewington's use of black and white pencil for the plant or other perching site, against which the beauty of the painted butterflies is seen to best advantage. The effect achieved, for example, by a mating pair of Black Hairstreaks (*Strymonidia pruni*) on a penciled blackthorn twig, of a male Purple Hairstreak (*Quercusia quercus*) basking on a an oak twig, or the once widespread but now endangered High Brown Fritillary (*Argynnis adippe*) perching on a bramble, selected for the title page, is brilliant. Life history stages are fully and elegantly illustrated, and the life cycle of each, the periods of the year occupied by each stage from egg to adult, is summarized in simple charts, precise to a week or so, attesting to the completeness of our knowledge of the phenology of these butterflies in their British and Irish localities. Where appropriate, the text is embellished with pencil drawings showing aspects of behavior—the courtship sequence of the Wood White (*Leptidea sinapis*), courtship and thermal orientation in the Grayling (*Hipparchia semele*), of ants attending a larva of the Adonis Blue (*Lysandra bellargus*), and others. I have long believed that F. W. Frohawk's illustrations could never be bettered: for seventy years this was true, but in my eye Richard Lewington has achieved this feat.

No apology for use of vernacular names in this book (or indeed in this review) is needed; these came into use with interest in the butterflies, sometimes changing across two centuries and more (without reference to any International Commission) and are an integral part of the history of these faunas, and of the English language. Moreover, the "popular" names have enjoyed a stability not shared by the Linnaean binominals—several long-familiar generic names having changed in recent years. The text is followed by suggestions for further reading, including guides to identification of British and European butterflies, general biology of these insects, and, in recognition of the important contribution made by local natural history societies in Britain, references to selected works on individual counties and other local geographical areas.

The book is published in association with The National Trust; it is well produced and printed, and remarkably inexpensive. It will be admired and enjoyed by all with an interest in butterflies, whether familiar with the faunas covered or not, by those with just a general enthusiasm for natural history and conservation, and by any student of the art of entomological illustration.

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THE LEPIDOPTERA: FORM, FUNCTION AND DIVERSITY, by Malcom J. Scoble. 1992. Natural History Museum Publications. Oxford University Press, 200 Madison Avenue, New York, NY 10016. xi + 404 pp., 321 text figs., 4 color plates. Hard cover, 18 × 25 cm. ISBN 0-19-854031-0. $78.00.

I cannot imagine attempting to summarize our knowledge of Lepidoptera in a single volume. Just think about the enormity of the task: there are monographs of most major taxa from one or more continents; books on the faunas of many regions; several butterfly books every year; an enormous literature on economically important species (e.g., more than 5,000 references on the Spruce Budworm complex), which describes most of what we know about larval diets, pheromone chemistry and correlated behavior patterns, diapause, population dynamics, predators and parasitoids, and many other aspects of Lepidoptera biology. Moreover, Lepidoptera often have been the subjects in lab studies, such as physiology and development, and in field studies, such as mimicry and speciation; they are the most diverse group of plant-feeding animals and therefore principal subjects of several books summarizing an extensive literature on insect-plant relationships and coevolution.

Scoble warns in the opening sentence of the introduction: "It is impossible to do justice in a book of modest length to a group of organisms as large, and with so complex a biology, as the Lepidoptera; so this volume is a summary and selective one at that." He accomplishes this by emphasizing the subtitled aspects: form, function, and diversity. However, I suspect many readers of *The Lepidoptera* will find themselves noticing what was not included and wondering why, rather than concentrating on the excellent summary of subjects that are treated.

The text is grouped into three parts: Part I, 5 chapters on form and function; II, a brief chapter on environmental and ecological importance of Lepidoptera; and III, a summary of diversity, in 5 chapters. Of these, the second is weak, but I think most lepidopterists will find the chapters treating morphology/function and the taxa to be extremely useful resources.

The sections on head, thorax, and abdomen of adults and on immature stages present synopses of morphology but emphasize function, so, for example, rather than just a description of thoracic anatomy, we are given discussions of wing folding, flight, migration, and diversity of color pattern; the larval description includes defenses against predators, diversity of food sources, and uses in classification; and structure of hearing, sound- and scent-producing organs are accompanied by their ecological and evolutionary significance and distribution in Lepidoptera.

In his review of diversity, Scoble copes with the extensive and rapidly changing recent literature on theories of relationships among higher taxa with a conservative approach. He presents a cladogram of relationships among primitive Lepidoptera, modified from Kristensen's 1984 review, so the several names that have been applied recently at the subordinal and lesser intermediate levels, such as Glossata, Exoporia, and Heteroneura, can be visualized, but he does not apply any of these in the text. Instead, Scoble recognizes 41 superfamilies, essentially all that have been proposed by Minet and others, and their included families. These he groups into four chapters treating Primitive Lepidoptera, Early Heteroneura, Lower Ditrysia, and Higher Ditrysia. A cladogram of relationships within Ditrysia ought to have been presented, comparable to that for the primitive taxa, so that readers might comprehend something about relationships among superfamilies within the unnatural groupings by chapters. Minet's 1991 classification of Ditrysia is cited but not applied in practice. Thus, Apoditrysia and Obtectomera are mentioned in the introduction to 'Lower Ditrysia,' but are not accorded status in the classification. An exception is Rhopalocera, which Scoble defines as a clade, emphasizing his theory of relationships of Hedyloidea as primitive butterflies.

The summaries of current literature (to 1991 in most instances) for individual families are well done. This likely will be the most useful aspect of the book for lepidopterists and other biologists who have not kept in touch with specialized taxonomic literature. Each superfamily is briefly characterized, followed by a synopsis of each family, and in some instances subfamilies, that includes adult and larval morphology, biology, and phylogenetic relationships. Often, only the most recent comprehensive work is cited, such as a chapter in Stehr's *Immature Insects*, and not the more specialized literature from which the information originates.

Often, too, it seems that the view is based on British or European concepts. Examples include: mention of yucca as a South American plant, a mistake that was made in the popular BBC TV series, *Life on Earth*; economic importance of Sesiidae mentioned particularly for raspberry and currant, based on British species, whereas the group has an

extensive literature on pheromones, biology, and control in relation to fruit and forest tree and squash vine borers in North America; the peculiar pupal 'legs' of ethmiids given as a defining character for the subfamily (citing Sattler's *Microlepidoptera Palaearctica*), a feature that is presumed secondarily lost in a major New World clade, described in my 1973 monograph. Among other imponderables, Scoble follows Kyrki's 1990 classification of Yponomeutoidea that distinguishes Ypsolophidae, including Ochsenheimeriidae, from plutellids, but he limits the biological summary to *Ochsenheimeria,* rather than the much more diverse and widespread *Ypsoloha*; omission of the *Lactura* group, which has been considered part of Yponomeutoidea but placed in Zygaenidae by Common in *Moths of Australia* and by Kyrki; and the moth illustrated as typical of Heliodinidae is *Pancalia nodosella,* a gelechioid, rather than the type species of *Heliodines,* which occurs in England.

The text is illustrated by excellent line drawings, along with SEM and micro photographs. The expressed purpose of Part III is to provide a guide to Lepidoptera diversity but not identification, and it is accompanied by 136 good half-tone photos of adult specimens, usually of one specimen judged to be typical for each family. Inconsistently, representatives of several subfamilies are shown for some families (Oecophoridae, Pyralidae, Arctiidae, Noctuidae) but not for other diverse families (Gelechiidae, Tortricidae, Lycaenidae) . The four color plates contain 34 photographs depicting living adults, larvae, and eggs.

Numerous generic and specific names are cited as examples in the text and in figure legends but without authors or reference to geographic regions, and none is indexed, so the family of a given insect has to be known to locate discussion of it. Biological features are well indexed (e.g., aestivation, courtship, boring/tunneling, leaf mining, migration, mimicry), and the Table of Contents is explicit, so search for non-taxonomic subjects is efficient. In some cases reviews of such subjects are split among different topics; for example, elements of yucca moth biology appear under modifications of the head in Part I, pollination in Part II, and Prodoxidae in Part III.

Any reader might nit-pick over particular subjects that have been omitted or slighted. Among the more surprising, I thought, was diapause, which is mentioned only in passing relative to migration patterns. Diapause certainly has been the key to life cycle adaptations by Lepidoptera in diverse climates and regions, not only winter at high latitudes and elevations, but in areas of seasonal drought, and in dry forest vs. lowland tropical forests at low latitudes. Lepidoptera exhibit countless fascinating specializations enabling different taxa to become diverse in regions of climatic stress, which has major biogeographical implications. Another major omission by choice is review of the importance of Lepidoptera in agriculture and forestry, which has motivated most of the studies leading to our knowledge of their biology and justified much of the funding of taxonomic research.

Nonetheless, this book does an admirable job of summarizing a vast and complex literature. I recommend it to every lepidopterist who is interested in morphology, diversity, taxonomy, or biology of moths and butterflies.

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BUTTERFLY FARMING AND CONSERVATION IN THE INDO-AUSTRALIAN REGION, by Michael J. Parsons. 1992. *Tropical Lepidoptera,* Volume 3, Supplement 1. Association for Tropical Lepidoptera, c/o Florida State Collection of Arthropods, P.O. Box 141210, Gainesville, FL 32614-1210. 62 pp. + index, 48 color photographs, text figures. Soft cover, 21.5 × 28 cm, ISSN (for *Tropical Lepidoptera*) 1048-8138. $18.00 postpaid ($10.00 for ATL members.).

Sometime after I returned from a 1977 consultancy in Papua New Guinea, I lectured on the experience at the Royal Entomological Society of London. Afterward, on the stair-

case to the dark-paneled library of that august body, roughly between the portraits of former presidents Charles Darwin and Alfred Russell Wallace, I was approached by an earnest young member. His name was Michael Parsons, and he was quite the keenest New Guinea enthusiast I had yet encountered. Unlike most collectors eager to go there, his desire was not fueled merely by his passion for birdwing butterflies, though he certainly had that. He seemed committed to going to New Guinea and learning everything he could about the island and its insects, and to enlist for their conservation.

Therefore, when I declined an offer to extend my consultancy with the Department of Wildlife, I recommended Mr. Parsons for the position. He was hired, and eventually spent over four years in Papua New Guinea on a series of missions. If he did not learn everything about the region's insects, he made a good start. He also created the research wing of the Insect Farming and Trading Agency, developed a manual for farmers, energized the overall program, set up a conservation and research project for *Ornithoptera alexandrae*, designed a superb set of butterfly stamps, and began a mapping scheme for the country's butterflies, among other efforts. Clearly, he was the right person for the job.

The work reviewed here is one of more than thirty to have come from Parsons' studies in Papua New Guinea (PNG) (*see* M. C. Morris' review of *Butterflies of the Bulolo-Wau Valley*, in *J. Lepid Soc.* 47:341–342). It actually consists of two papers bound together to make a book in the form of a supplement to *Tropical Lepidoptera*, Volume 3. The first part, "Butterfly Farming and Conservation in the Indo-Australian Region," gives a detailed and extremely useful summary of this increasingly visible and important field. The second half, "The World's Largest Butterfly Endangered: The Ecology, Status and Conservation of *Ornithoptera alexandrae* (Lepidoptera: Papilionidae)," speaks for itself.

Part One introduces, defines, and summarizes the origins and practice of butterfly farming. The introduction makes a strong statement for sustainability, and raises the vital question of whether this renewable resource actually can be used to save tropical forests. Next, the author details the history of study and collecting in the region that led to the demand for specimens, and traces the evolution of the PNG model of meeting this demand. He examines the government rationale and policies for the Insect Farming and Trading Agency (IFTA), and explains the benefits of a successful system for both villagers and customers. Economic reform (with profits going to locals) and incentives for both conservation and reforestation clearly can arise from such a program, if successfully carried out. Parsons argues strongly for research and extension work to support such programs, and explores the kinds of financial figures that can be involved. The economics of IFTA are examined in some detail. In fact, the bulk of the paper is devoted to and drawn from the PNG experience. However, Parsons also discusses the butterfly trade in Taiwan, Malaysia, and China, and what he calls "failed take-offs" in the Solomon Islands, Indonesia, and India.

Not content to leave the subject on an ideal basis, the author presents and dissects a number of "myths and misunderstandings." He takes on the issue of collecting versus farming, and finds that overcollecting is probably irrelevant to most species. He examines the actual extent of farming, coming to the conclusion that it fluctuates widely and, in practice, is far less than some magazine writers have represented. He looks at the "ideal" butterfly farm versus its usual state in reality. And, at length, he teases apart what he calls "a tangled web of legislation" to find that laws, regulations, and treaties usually interfere more with farming and orderly trade than they help with meaningful conservation. The discussion of CITES (the Convention on International Trade in Endangered Species) and its Machiavelian application to *Ornithoptera* species is especially helpful history although maddening to read. In fact, the author's frustrations come through frequently in this long paper, not the least with respect to his Chinese consultancy. Nonetheless, the long conclusion shifts subtly from a plaint for adequate funding and sensible application of knowledge, to a hopeful insistence that "the time is apparently right to integrate butterfly farming into many tropical forest conservation plans."

The second part concerns the biology and management of Queen Alexandra's Birdwing, the world's largest butterfly. Although discovered in 1906 and recommended for protection since at least the 1960s, this extremely narrow endemic has lost most of its prime habitat and lives today in severe jeopardy of extinction. Parsons tells the history of the species'

decline in riveting detail. Through a combination of volcanic eruption, ancient grass-burning practices, subsistence gardening, wartime airstrips, oil palm plantation, and logging, the animal's obligate forest and host *Aristolochia* vines have become fragmented and scarce.

Ornithoptera alexandrae was first gazetted for protection in 1968 upon the recommendation of Joseph Szent-Ivany. Ramon Straatman was contracted to survey the insect and recommend a conservation program in 1970. When Sally Hughes and I finished our consultancy in 1977, we recommended to IUCN that it be made a world priority species, and this was later confirmed in the *IUCN Invertebrate Red Data Book*. In 1980 Parsons developed a detailed set of preserve recommendations. Yet despite all this and more, much of the butterfly's forest habitat was aggressively logged, not without government and local blessing, between 1983 and 1987. When Parsons returned, he had the distinct displeasure of resurveying former habitat now made wholly unsuitable.

For complex reasons that the author explains in admirable detail, the conversion of *O. alexandrae* habitat through oil palm plantation and logging continues even as the government declares repeatedly its intention to save this species, one of seven declared National Butterflies as well as the symbol of Oro Province, where it occurs. Traditional rights of land tenure, coupled with the temptation of quick cash from foreign investors, have defeated all efforts to date. One could have forgiven Parsons for turning his back on what must have been an extremely frustrating endeavor. However, he returned in the early 1990s to perform a new survey (funded by Conservation International) and to create an action plan (commissioned by the World Bank) for the integration of oil palm development and birdwing conservation. This paper outlines the findings of both documents.

Parsons believes the world's largest butterfly can still be saved, but only through concerted action, involving education, local and national agreement on habitat protection and management, and sustainable farming of *O. alexandrae* to provide locals with a stake in the forest it requires. This latter goal has long been suggested and hoped for by almost everyone involved, but the special status of the butterfly has always prevented it—a case of supposed "protection" blocking actual conservation.

Papua New Guinea was once known for its ambitious stance toward wildlife conservation, its national constitution even naming insect protection as a goal. Recession, custom, and the temptations of foreign capital have all combined to enfeeble these objectives. As Parsons concludes this section: "An *O. alexandrae* Conservation Project may provide a means of, once again, putting the National Goals into practice." We must all hope that his well-crafted plan has a real chance to work, and be grateful for this fine account of an exceedingly difficult and important problem in biodiversity conservation.

Parsons' labors in the Melanesian fields have been so fruitful that I wish I could leave this review with summary and praise. However, perhaps in part due to his very fecundity, the work is studded with flaws that merit mention. Most serious among these are omissions of consequence. The paper lacks any reference to the *IUCN Invertebrate Red Data Book* or indeed to any IUCN sources other than the swallowtail red data book and action plan, though it was IUCN's influence that brought prominence to the PNG undertaking. He fails to mention either M. G. Morris' Churchill Fellowship to examine butterfly farming throughout Oceania or a National Academy of Science panel that visited PNG to report on the state of butterfly and crocodile farming, though he cites their reports. He refers to an "EEC mission" but never explains what this is. His treatment of the situation in Irian Jaya is thin in terms of recent developments, and the same can even be said for PNG, where much of his information might have been updated through consultation with manager Peter Clarke. Parsons nowhere mentions Wings for the Earth, a California-based non-profit engaged in promoting butterfly farming. His discussion of CITES, though extremely helpful in these rule-conscious times, neglects to define what its several appendices actually require until quite late in the second paper. Also notable in its absence is any reference to the work of Larry Orsak, who has been engaged in butterfly conservation projects in PNG for a decade. True, Orsak's paper "Killing Butterflies to Save Butterflies: A Tool for Tropical Forest Conservation in Papua New Guinea" (*News Lepid. Soc.* May/June 1993:71–80) appeared after the present paper, and his 742-page report on conserving *Ornithoptera alexandrae* is dated 1992, so Parsons probably had not seen it. How-

ever, it is unlikely that Parsons was unaware of Orsak's contribution, or his consultancy for the government of PNG (through the Wau Ecology Institute) to prepare an action plan for the butterfly's recovery. One is naturally curious how this plan relates to that prepared by Parsons for the same government.

Whether or not Parsons felt himself competing with Orsak for currency of publication, the papers do carry the unfortunate appearance of rushed production. The poor editing is dramatic, or rather, the absence of editing. With all of his impressive findings to report, the author should have been able to count on assistance when it came to copy-editing, but he seems to have received none. The paper is rife with repetitive misspellings ("truely," "intergrated," etc.) , cumbrous language, orphaned referents, misplaced modifiers, fractured grammar and syntax, skipped and superfluous words, and so on. Carelessness creeps in, as "In PNG, many hundreds of swallowtail species . . . are also collected." Or, "Countries like New Guinea"—there never was a country called New Guinea, and there is certainly no place "like" it. Irian Jaya has "competative monopolies"—a misspelled oxymoron. There is a confusing plethora of acronyms, often used many pages away from the definition. Four plates of splendid color photographs are unnumbered, leaving the reader to guess at matching captions. (Despite the title referring only to butterflies, four of the eight cover photographs depict moths; but faced with Parsons' spectacular photos, one can't quibble.)

The language veers toward the turgid. Some quotations are cavalier: I am quoted referring to butterfly "dead stock," a term I have never used. The author indulges some quaint and dated terms (logging with "airships"?; "Washington, USA") and arbitrary capitalization ("World Economy," "World Economic Recession") . British and American usages alternate at random. The text is repetitive, wordy, and could be cut by one-third to its advantage.

In short, it is sad that such a fundamental source as this is bound to stick in the eye and the mind for its rough-draft nature. It is not required that remarkably accomplished lepidopterists also write with polish; but if they do not, it is required that they receive the favors of a good editor before they are hung out to dry. If the editor of the journal in question (in this case John B. Heppner, another prolific and highly talented lepidopterist) is too busy to do it, then outside editorial assistance should be sought. If these papers were indeed peer-reviewed, that process also was entirely too casual.

Parsons distinguishes between high value/low volume specimen trade and low value/high volume trinket trade, but then mixes them up like apples and oranges. He mentions private concerns in PNG, but not their legal ramifications or how they are likely to affect IFTA. The Taiwan section is somewhat muddled, and the Malaysian statement hyperbolic; references ranging in rigor from science to Sunday supplements are given equal weight. If the level of farming in Irian Jaya is as low-level as he says, are the many birdwings in trade from there all wild-collected, in contradiction of their ads? If collecting is as harmless as he states, where is the sense in saying that "the evidence . . . furnishes proof of the benefits of collecting to satiate, and thereby beneficially suppress, their market demand?" This seems both circular and specious—if a species such as *Trogonoptera brookiana* is not being overcollected (as it may well not), how can satiation of the market through collecting be beneficial? Again, Parsons later speaks of farming rarer species as providing a "beneficial decrease in their desirability;" yet this follows a strong argument that collecting is benign. He seems to be seeking a rationale for farming in a danger that he has himself defused. Parsons usefully criticizes legislation, but fails to mention its early value in cutting back the iniquitous black market; or the unusual population biology of *Ornithoptera*, making them somewhat more vulnerable to collecting than most insects. Similarly, the historical rationale for adding birdwings to Appendix II of CITES—to monitor world trade—is not discussed.

Even hurt by careless editing, the value of this work far outweighs its difficulties. Parsons was the right person in the right place to stimulate butterflies as a sustainable resource reform, while dramatically adding to our understanding of the biological nirvana we call New Guinea. His grand summary of the results, partially self-funded for its publication, provides an essential reference to all those interested in butterfly farming. It will necessarily serve as the basic resource in the field. Revised, edited, updated, and printed

in a handier format, it would stand even stronger as a classic in the ever-growing field of butterfly conservation and sustainable development. Either way, I'm glad Mike Parsons went to Papua New Guinea and came back to write about it, and I hope he will go again and be given the chance to follow through on his recommendations for *O. alexandrae*. His strong call for real habitat conservation instead of deflective regulations is heartening at a time when bureaucratic reaction to sampling intensifies. And his call for all lepidopterists to "adopt a policy of actively caring for the 'goose that lays the golden egg'" is something we certainly need to hear and heed.

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BUTTERFLIES AND CLIMATE CHANGE, by Roger L. H. Dennis. 1993. Manchester University Press, Manchester. 301 pp., 25 × 38 cm. Hard cover, ISBN 0-7190-35058, £50 (about $80 US); soft cover, ISBN 0-7190-40337, $39.95 US (distributed by St. Martin's Press, New York, NY).

The day my review copy of *Butterflies and Climate Change* arrived, I happened to commiserate with a colleague about the poor intellectual health of ecology. I complained that almost every other branch of biology had progressed more in the past 25 years than had ecology. "True," she said, "and the biggest breakthrough ecology *has* made is the rediscovery of history."

Since the eighteenth century, biogeographers have recognized that the distributions of plants and animals have two components: history and ecology. History determines whether an organism has the opportunity to live in a place: ecology, whether or not it does. Somehow this simple truth evaded a whole generation of ecologists, who in their search for mathematical elegance in the structure of the biosphere had no taste for the messiness of historical contingency. But it forced itself on them; for lack of it, their oversimplified research program failed. Now history is suddenly trendy. Roger Dennis is to be congratulated for doing ecohistory long before it became trendy.

The British Butterflies: Their Origin and Establishment (E. W. Classey, London, 318 pp.), Dennis' first major excursion into ecohistory, appeared in 1977. That happened to be the centenary year of Samuel H. Scudder's first paper on the fossil insects of the Scarborough Bluffs, a paper generally considered the beginning of paleoentomology as a discipline. When Scudder died, he was eulogized (in *Science*, 1911) by T. D. A. Cockerell as the entomological equivalent of the three great vertebrate paleontologists Leidy, Cope, and Marsh combined. We lepidopterists tend to remember Scudder as one of the nineteenth century's greatest butterfly workers. He combined his two passions in early studies of fossil butterflies and attempts at lepidopteran phylogeny reconstruction. As a former student of Louis Agassiz, the intellectual father of the Ice Age concept, Scudder was very aware of the heavy hand laid by the glaciers on the New England landscape, and he speculated on Pleistocene influences in butterfly biogeography. It was he who told and retold the tale of the White Mountain butterfly, *Oeneis melissa semidea*, as a living relict of the Ice Age. Nothing much happened in butterfly ecohistory for the next 90 years.

Meanwhile, paleovegetational reconstruction advanced; palynology (study of fossil pollen in bogs and other environments) and the study of plant macrofossils made immense conceptual and methodological strides. Beginning in the 1960s and largely as an offshoot of archeological digs, paleocoleopterology—the study of fossil beetles—joined paleovegetation as a tool for reconstructing ecohistory. This work, pioneered by G. R. Coope and H. K. Kenward in England, attracted little attention at first. Meanwhile, no one was finding rich troves of fossil butterflies in peat or early man's kitchen middens, and butterfly biogeographers seemed preoccupied with the then-trendy question of why there were so many species in the tropics.

Because we lacked real fossil data, butterfly workers were reduced to the role of consumers of the stuff palynologists, paleobotanists, and eventually paleocoleopterists would produce. But by the mid-1960s it had dawned on some of us that we could use that stuff to try to understand butterfly distributions in temperate and high latitudes. The first major breakthrough was *Geography of the Palearctic Papilionoidea* by A. S. Kostrowicki, published in English in Warsaw in 1969 and to this day read by almost no one. In 1970, before I had heard of this book, I published a little paper (*J. Res. Lepid.* 9:125–155) on the historical biogeography of North American skippers associated with sedges. I remember wondering as I did this work why no one had thought of doing it before, when there was so much ecohistorical information out there.

Roger Dennis did the same thing, but for the *entire British butterfly fauna*, in his 1977 monograph. I should have reviewed that book in this journal but didn't. That, however, is probably not the reason it failed to create much of a stir; ecohistory was still on the fringes of respectability in 1977. Now it is "hot," and with a title like *Butterflies and Climatic Change* Dennis and the publishers can hope for healthy sales to the diverse group of scientists and amateurs preoccupied with global warming and other signs that the Last Judgment is nigh. Those who buy this book knowing nothing about butterflies will know a great deal when they are done reading it.

In it, Dennis seeks to define a conceptual structure in which butterfly-climate relationships can be analyzed, and then to use it to forecast the future of the British fauna. The first 40% of the book (Chapters 1–3) is devoted to this conceptual structure. It constitutes a quick lesson in meteorology and climatology, followed by a condensed textbook of butterfly biology with particular attention to coloration, thermoregulation (behavioral and physiological), and other topics Dennis considers relevant. He covers more butterfly ecology than is needed to make the point that butterflies are very vulnerable to density-independent mortality factors, i.e., weather. Some of the topics, such as pattern ground plans and ontogeny, are really extraneous and many have been better and more thoroughly covered recently elsewhere. The treatment of atmospheric processes, microclimate, and heat transfer is broad and inescapably superficial. These are quantitative topics not easily explained without mathematics—even a gifted writer like Bernd Heinrich has trouble—and Dennis has probably done as well as can be expected. He does steer us to sources, and, for the sophisticated, some of these, such as Joel Kingsolver's work, are a sheer delight; those who flunked or never took college physics need not pursue them.

The heart of the book is to be found in Fig. 4.3 (pp. 146–148), captioned "Colonization, extinction and evolution of British butterflies during the last glacial-interglacial hemicycle," and Table 4.1 (pp. 154–157), "Historical data for resident British butterflies for the last deglacial hemicycle." These are somewhat updated summaries of what was in the 1977 book, intended to allow us (in Chapter 5) to extrapolate to the future of the British fauna. Lacking our great-grandchildren's hindsight, we can still try to evaluate Dennis' claims by examining the assumptions he employs in arriving at them. After all, there are no fossils: past butterfly "data" are pseudo-data.

Dennis is aware that what he proposes to do is risky. On page 144 he states (correctly) that climatic correlations with species boundaries do not prove causation. Yet to do what he wants to do, one has little choice but to act as if they do. It is even more dangerous to assume that climatic adaptation is static in time. Paleocoleopterists and palynologists often act as if congruent morphologies imply identical climatic adaptations, but they know better. They know, for example, that pack rats in the southwestern United States just sat there, adapting repeatedly to the radical changes in climate and vegetation going on around them for millennia. They know too that many morphospecies of both plants and animals contain "ecotypes," ecological races which may be very different physiologically despite a complete lack of apparent markers. Suppose one found an isolated fossil *Papilio zelicaon*. Was it a multivoltine *zelicaon* from a subtropical-Mediterranean climate like San Diego's, or did it live at tree line? If it is found with other organisms they might be useful in defining the climate. But those who do this kind of work have had to admit the reality that multispecies paleoassociations sometimes combine forms with seemingly incompatible ecologies today—meaning either the prior existence of novel ecotypes or different climates from those extant today, or both.

Lacking fossils, Dennis has to use paleoclimatic reconstructions and knowledge of the climatic adaptations of extant species to try to reconstruct butterfly paleofaunas. This is more or less the inverse of what ecohistory data producers do, and it has no obvious reality checks.

In 1994 Scott Elias published *Quaternary Insects and Their Environments* (Smithsonian Institution Press, Washington, DC, 284 pp.; reviewed by B. Drummond in *News Lepid. Soc.* 1994:77). There is almost nothing about butterflies in it, but it should be read by everyone who reads the Dennis books. The mountains of paleocoleopterological data give us a fine lesson in humility. (The only pretenders to truth who fare worse than ecohistorians and paleoecologists are vicariance biogeographers.) The biggest problem turns out to be not changing climatic adaptation by morphospecies but vagility beyond our wildest dreams. An endemic Sicilian beetle with nothing at all to suggest it had ever been anywhere but Sicily turns out to have been in Britain during a warm interglacial. A related beetle now confined to the Tibetan Plateau was in Britain during a periglacial stage. And so on. How can we retrodict faunas when we cannot define the pool of potentially available players? Similarly, how can we hope to predict future faunas? The lack of fossils makes butterfly workers dependent on a handful of bizarre relicts to remind us how feeble our imaginations are. The fact that *Vanessa indica,* a patent relict in the Canary Islands and Madeira, was rationalized away as a recent introduction in commerce (Leestmans 1978, *Linneana Belgica* 7:130–156; Shapiro 1992, *Entomologist* 111:10–21) is a case in point.

Butterflies and Climate Change is a well-produced book. It is nearly free of typographical errors; I noted five plus a serious *lapsus calami* (*Colias* for *Colotis* on p. 207). The text is very dense and cannot be read casually. The bibliography is huge—some 1100 entries—and eclectic, but in some ways unsatisfying; hardly any non-English-language works are cited, and it is surprisingly light on paleoentomology (three Coope papers, no Kenward) and on the conceptual framework of paleoenvironmental reconstruction. On the other hand, it cites very recent theoretical papers in ecology and, as noted above, could even be used as a short text in butterfly biology in general. The fact is that once one begins doing a work like this, the limits to one's coverage eventually become arbitrary and highly personal. Had I written this book I would have a somewhat different, but no "better," set of " in" and "out" topics and citations.

I have only one public complaint about interpretation: on page 169 Dennis seems content to accept Shields' claim that all the butterfly families were already in existence in the Mesozoic. This may be true, but there are no fossils to support such a claim. It is strictly a backward extrapolation of evolutionary rates. But does anyone think rates of *adaptive* evolution are constant in geologic time?

Dennis is to be congratulated for an important achievement, even if I doubt the British fauna will behave predictably. It was G. K. Chesterton who described (in *Napoleon of Notting Hill*) the game of "Cheat the Prophet," in which the young people listen respectfully to the predictions of the sages, wait until the sages die, and then do something different. Perhaps British lepidopterists will need updated versions of Torben Larsen's Mid-East or tropical African butterfly books to identify the fauna of gardens in South Kensington!

One final observation: modern biochemical-genetic techniques ("phylogeography" or "genography") as applied to historical biogeography are rapidly rendering work of this sort obsolete. Arm-wavers like Dennis and me will have to go molecular or join an increasing number of butterfly species in oblivion.

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BUTTERFLIES THROUGH BINOCULARS: A FIELD GUIDE TO BUTTERFLIES OF THE BOSTON-NEW YORK-WASHINGTON REGION, by Jeffrey Glassberg. 1993. (Forward by Edward O.

Wilson, Preface by Robert K. Robbins.) Oxford University Press, 200 Madison Avenue, New York, NY. 160 pages, 300 color photographs in 40 plates. Soft cover, 14 × 21 cm, ISBN 0-19-507983-3, $19.95.

A few years ago Jeff Glassberg called to tell me that he and some others were starting a new organization to be called the North American Butterfly Association, to be devoted to butterfly watching and appreciation. As a twenty-year proponent of this underrated activity, I was pleased to hear it. He went on to inform me that the group would be undertaking a new list of common names for American butterflies, and asked if I would be willing to sit on the committee. Since I had initiated the joint Xerces Society–Lepidopterists' Society Common Names Committee in 1980, and took part in the arduous and contentious task of constructing a synonymy and list of such names, and since *The Common Names of North American Butterflies* had only recently been published (1992) by Xerces and the Smithsonian Institution, under Jackie Miller's inspired leadership and editing (see review by R. R. White in *J. Lepid. Soc.* 46:310–311), I replied that I would be happy to help the new group in any other way, but that there were several tall buildings I would rather leap off than to be on another common names committee.

In spite of what I considered a monumental redundancy, NABA has indeed come about and has begun publishing the impressive magazine *American Butterflies*, co-sponsoring and conducting the Xerces Fourth of July Butterfly Counts, and promoting butterfly awareness. For this, Glassberg is to be congratulated. He also deserves praise for his new book, a manifesto of the butterfly watchers' creed and a guide to doing it in the northeastern states. *Butterflies Through Binoculars* takes this delightful avocation to a new level.

The cover copy of the book says, "while traditional guides cater to the collector, offering drawings of captured and mounted insects, this book provides photographs of *living* butterflies in their natural poses and in the correct size relationship to other species, making identification quick and easy." Other advertisements for the book have actually stated that this is the first book to do so. That, of course, is wrong. Areta A. Saunders used photographs of live butterflies as long ago as 1932, in her *Butterflies of the Allegheny State Park.* My *Watching Washington Butterflies* (Seattle Audubon Society, 1974) and *Audubon Society Field Guide to North American Butterflies* (Knopf, 1981) both employed photographs of live butterflies and a watchers' standpoint. And Paul Opler and George Krizek's *Butterflies East of the Great Plains* (Johns Hopkins, 1984) also used photos from nature. So Glassberg is far from the first to take this approach. However, he has made many improvements over previous treatments and produced a near state-of-the-art effort. Besides, authors should not be held responsible for publishers' flak.

Let us now take a field trip through the field guide and see how it works. The clever cover shows two bright beauties as if through binoculars, inviting you in. The title is inspired, the subtitle unwieldy; it might have benefited from one of the nicknames for the region (Bosnywash, Bos-Wash Corridor). The region covered, excluding Long Island and outer Chesapeake, is small enough to treat in detail. I like the idea of addressing the resource near where most of the people live, rather than taking the view that would-be watchers must travel to distant wildlands.

The endpapers contain twelve black silhouettes representing seven "families" to be encountered in the book's range. This tool, borrowed from early Peterson guides, might help novices learn to recognize "type" more readily from the basic shape of the subject.

The text begins with brief commendations by Big Guns. E. O. Wilson's Foreword speaks with grace of the impulse that leads us into these Elysian fields: ". . . to re-acquire a sense of timeless languor . . . to be free in a world without destruction or pollution, an aurelian again!" He characterizes the book, aptly enough, as "a people's natural history," user-friendly, and an open door. Robert Robbins' Preface predicts an "explosion of interest in butterflies," something that is already coming true and which Glassberg's book is poised to assist.

The author's copious acknowledgments conclude with a switch delightful for its attitude if not its syntax: "If you find something you find objectionable in this book, please randomly choose one of the above reviewers and assign the responsibility for the error to

them." This fairly represents both the prose (workmanlike) and humor (good) of the following 160 pages.

The first twenty comprise an introduction telling how to use the book. "How to Find Butterflies" is a bit brief and vague, but complemented by later habitat descriptions. "How to Identify" gives a good, clear opening to this demanding part of the practice. The important sections on "Binoculars" and "Photography," although adequate, are very general. For a book with such an emphasis as this one has, more detail and brand comparison would have been warranted and helpful. Enthusiasts will quickly outgrow these curt remarks and wish for more of the author's experience. The advice, what there is of it, is good, solid, and clear.

"Butterfly Lives" is still more concise, as is "Butterfly Gardening," followed by short lists of garden species and nectar sources. The detailed understanding, it is implied, will come through your own observation. The two remaining text sections, however, are treated in more detail, and appropriately so. First, Glassberg assays "Migration" within the book's corridor. In addition to classic patterns of movement, he mentions the lesser-known phenomenon of nymphalids moving south in large numbers in the fall, citing his observation of some 16,000 butterflies of four species passing Brooklyn in one day. His theories are intriguing, though he fails to mention the buckeye as a major mover: that's the one I saw mobbing Cape May along with the southbound warblers and accipiters. He also perpetuates the erroneous belief that most of the California monarchs overwinter near Pacific Grove, but the migration section on the whole is a welcome plea to the many new watchers for further investigation of this murky subject.

The section on "Conservation" stresses the preservation of habitat and diminished pesticide use and pollution. Glassberg envisions "an interconnecting network of small protected habitat units along with a few larger units," which (if carefully chosen) he feels would suffice to protect most of our butterfly species. Those who have been concerned about NABA's approach to collecting will be interested in Glassberg's statements on the subject, to which he devotes one paragraph. He does believe that collectors, operating without scruples, are "capable of having a significant negative effect on butterfly populations." He cites Mitchell's satyr (*Neonympha mitchellii*) as an example, stating that it is "almost certainly gone from the northeastern United States, extirpated by relentless collection pressure." Nowhere does Glassberg proscribe collecting as such, although Wilson, in his Foreword, equates putting away the net and pins as having "matured to the level of birders." Neither author mentions that the range data upon which all conservation activities are based owe almost entirely to the activities of collectors. Wilson later says that "butterfly biology is in an early stage of exploration," with a great deal left to be learned; but fails to make clear for the reader that such knowledge will again rely on the immatures who still collect. Nor is it explained that learning butterfly identification comes faster for those who maintain a reference collection, and that strict watchers will experience frustration trying to achieve the powers of recognition that their collecting friends have long since mastered.

We come then to the species accounts, which are the heart of the book. At first glance these resemble every other attempt to personify a creature in a few telegraphic paragraphs, but there are some real innovations here. Some work better than others. Each account includes the following features: name, size, similar species, identification, habitat, range, specific localities, flight period and abundance, major foodplant(s), and comments. Each of these bears examination for its treatment.

Name. Glassberg explains why he started the committee I declined to join, and uses its recommended names in all cases, sometimes giving alternatives from other field guides. To be fair, some of the committee's departures are improvements. On scientific names, the author discusses a couple of reasons for differences among authors (omitting several reasons) and calls the ICZN gender guideline "a rule only a pedant could love." He fails to identify the authority he follows for scientific names, nor does he designate authors or subspecies.

Size. The author recognizes radical variation in size among individuals of a species, then goes on to adopt a peculiar method of size description involving "size standard" species. So when we look up Dion skipper, we read that it is the size of the Zabulon/Hobomok

skipper. We have to go to Table 1 to see that this equates to 10/16 inches. Some are ⟨ or ⟨⟨, others ⟩ or ⟩⟩ than the standards. Yet we already know that they all vary, and not necessarily proportionately. From its cumbersome method of secondhand comparison to its quaint sixteenths of an inch, this is not the most successful section. This innovation offers nothing over the good old "23–33 mm" system, or even "small/medium/large."

Similar Species. These do not always correspond. For example, the cabbage white is similar to the checkered white, but apparently not the reverse. Confusingly similar species are sometimes overlooked. For example, many beginners confuse female eastern tailed blues with hairstreaks, a fact not noted here.

Identification. These chatty descriptions nicely capture the looks and sometimes the key behavioral quirks of the species. The jacket hype promises "entirely new field marks" for identification; a tall order this, and I was skeptical. I compared ten confusable species against Klots, Opler, and Pyle. This exercise turned up four new field marks to six established ones—not bad.

Habitat, Range, and Specific Localities. These sections give useful summaries of the species' occurrence—overall, throughout the region covered, and within the local landscape. Unfortunately, the latter section only appears in a minority of accounts—those that are "rare and/or local in one of the subregions," but not so rare as to be liable to what Glassberg calls "the substantial danger of butterfly collectors destroying the localized colonies."

Flight Period and Abundance. These notes are given for each of the four subregions, which correspond to the vicinities of the four major cities that define the region: Boston, New York, Philadelphia, and Washington. Glassberg notes that this is only a rough guide to variable conditions. Maximum numbers seen are given for some species and regions, though only sporadically and to uncertain ends: does it tell us anything, or just brag on the author's big days? This feature could use interpretation and more uniform application.

Food Plants. This completes the profile of the species whereabouts. Favored nectar plants are sometimes named.

Comments. Glassberg honestly states that "Here I include remarks of an unpredictable nature;" and about his more lyrical comments, he advises that we may either "accept these at face value, or view them as having been written with an ironic sense of detachment, laced with a nostalgia for an imagined simpler time." If he was nervous about losing his objectivity here, he should have relaxed and done it more. The comments, where they appear, offer some of the best reading in the book. Whether speaking of "hundreds of [Cabbage] Whites dancing around the blooming Purple Loosestrife" or the Gray Comma, "often overlooked because it is most common in woodlands in October when butterfliers become rare," Glassberg broadens our view of the species in question when he indulges his own responses. Writing field guides is the art of balancing between the objectively descriptive and the personal reaction of the writer. When the latter is lost, the book becomes more sterile. For example, the classic Klots Peterson Field Guide was full of personalia, including egregious puns ("*Nysa* is very nysally distinguished from other *Amblyscirtes* of our area by the distinctive underside pattern," etc.) With many more border species to cover, the Opler/Malikul replacement lacked the room for much in the way of authorial comment. The result is a superb guide but a diminished read. Glassberg's own comments are highly erratic. Among the swallowtails, only the black and the tiger rate comments. Skippers get very few overall. I would like more. It is through these asides that we can appreciate the author's individual lens on the subject, and Glassberg's is a sharp and colorful view to be enjoyed, when he unveils it for us.

Six appendices follow, making up about a third of the book. Appendix A offers Descriptions and Checklists for Selected Butterflying Localities. This excellent section includes detailed profiles of nine good butterfly-watching spots known for their diversity, abundance, and accessibility. Each gives a description of the site, a run-down on its butterflies, a list of species to be encountered, and directions, written up by persons familiar with the local conditions. Brief notes follow for 37 additional sites. This will be one of the most useful parts of the book for many, though collectors should note that butterflies are protected on most of the sites mentioned.

Appendix B gives both the median and ranges for flight periods of New York area

butterflies. Appendix C conveys the same information graphically, adding the factor of abundance, through an ingenious form of phenogram. These break down the occurrence of New York area butterflies into five-day blocks over a five-year period, as expressed by black bars of three thicknesses for uncommon, common, or abundant. I like these diagrams very much, as they express so much data so compactly. Their chief problems are two: though the data are attributed to the New York Butterfly Club, we are told nothing of the nature, location, or status of the data base itself. And the five years represented are not designated (is this 1875–80 or 1987–92, or what?) so that no comparisons are possible with climatic records, Season's Summaries, or other information. Clearly, the seasonal appearance and abundance of species will vary up and down the corridor of the book's concern. Still, these appendices will give field trippers a good idea of what to expect.

Appendix D is a checklist of the species known to occur in the urban-coastal strip, giving English names only. Many users would prefer to see scientific names here as well. Appendix E lists butterfly societies and clubs. Appendix F usefully lists the Xerces Society's (now NABA co-sponsored) Fourth of July Butterfly Counts that take place regularly within the book's area. Impressively, this now totals 25 annual outings, and counting.

The text wraps up with a glossary of terms used, all anatomical except for the quirky inclusion of the genus *Andropogon*—ecological and biological additions would have been welcome; a worthwhile, if brief, bibliography; photo credits; and an index to species, in both English and Latin, but giving only the primary page-mention.

The forty color plates of butterflies photographed from life complete the book. Their captions, on the opposite page, give both scientific and vernacular names; tell where and often when each was photographed (this is to be applauded); reiterate the chief field marks; and apply an abundance rating for each subregion. Different forms, sexes, and orientations (dorsal, ventral) are often depicted. On the whole, the photographs are excellent. None are obviously manipulated, but for one pinned specimen. Focus is generally sharp, but occasionally sacrificed for sake of inclusiveness. Some of the subjects are worn—the mourning cloak will not break any hearts—but that's nature, and some of the best of contemporary butterfly photography is highlighted here. Several pages have gaps, and one wonders whether the space might have been well filled with additional clarifying images or representative larvae.

Derivative of Peterson, black lines point out field marks; however, not only do these sometimes interfere with the image, but they have been used only fitfully, and, unless I'm missing something, arbitrarily. Likewise, sex is often indicated but not infrequently omitted, even when it is obvious. The words sometimes do poor justice to the images, such as calling the subtle lilac-silver of the gemmed satyr a "gray patch," or the hyaline spots of *Erynnis* spp. "white." Skippers are not stinted here. Though they will be daunted at first, diligent watchers should be able eventually to identify most of their Bosnywash butterflies with their binoculars and the aide of this book.

It remains only to make a few general comments and specific corrections. The text would have gained from more consistent and rigorous editing. Jawbreaker jargon ("significantly facilitating") butts heads with a looser, more pleasant voice ("preview your space in heaven"). Overgeneralization plagues the book. Glassberg describes lawns as deserts, but this need not always be true—we all know lawn skippers, blues, and sulphurs on the right kind of lawns—the point is that chemically treated, overmown lawns are impoverished. Likewise, powerlines are recommended as attractive habitats. True, unsprayed lines can be very good, but others are maintained with herbicides and offer little to the lepidopterist. I would have welcomed these kinds of specifics. The "field marks" concept should be credited to Roger Tory Peterson, who both coined the term and popularized its use. Glassberg encourages readers to keep lists of what they see and where, but this is too vague. He should give minimum data needs, including *detailed* date and locality description, and explain why this is important (butterfliers can contribute valuable data). What about notes on behavior? And where can observers "send it in?" State natural heritage programs, butterfly surveys, etc., rely on amateurs' field observations; this should be noted and aided. Watching will never begin to replace catching as a tool for knowledge and conservation until watchers become adept record-keepers, like many birders. In metamorphosis, moulting "will happen a number of times." Why not be specific: "occurs four

to six times." The statement that some species can overwinter in any stage needs documentation. The author ignores watching without binoculars, and catch-and-release, both very important to versatile and successful butterfly watching as well as to teaching. Learning to identify butterflies comes much faster through careful capture, forceps-exam, and release (which need not injure the animal) than through mere "binocularing."

As with any ambitious book, one could continue to find minor faults until the butterflies come home. However, though it could use some refitting for the second edition, this book's strengths outweigh and outnumber its faults. When Jeff Glassberg made his self-styled apotheosis from collector to watcher, he decided to take as many with him as he could, and to attract the multitudes who, until now, have been mired in the quotidian of birds and wildflowers. Happily, he has done so with style, and without actually denigrating collecting *per se.* He has certainly acted on his convictions, first by founding NABA, and now with this book. I have no doubt that lepidopterology will benefit from a broader public, whatever their chief form of pursuit, so long as they are mutually tolerant and considerate. And I have no doubt that, because of this book, butterflies will win many more devotees among the most densely packed parcel of our populace.

Oxford University Press has produced a handsome, solid, and well-priced volume that is sure to enhance appreciation of a resource undervalued until recently. Lepidopterists will want it as well as those just discovering butterflies. I only wish I'd had it during the three years I spent in New Haven.

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BIOLOGY AND CONSERVATION OF THE MONARCH BUTTERFLY, by Stephen B. Malcolm and Myron P. Zalucki (editors). 1993. Natural History Museum of Los Angeles County, Science Series No. 38. Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007. 419 pages, 2 color plates, numerous B&W photographs and text figures. Hardcover, 18 × 26 cm, ISBN 0079-0903. $90 (+ $9 p&h).

In the Introduction to this volume, the editors, Steve Malcolm and Myron Zalucki, suggest that the Monarch butterfly and its relationships to the biotic and abiotic environment provide a valuable model for investigating a range of questions in all aspects of biology. It was exciting and encouraging to look over this book and realize just how much this butterfly species, its relatives, and its ecological and evolutionary interactions have contributed to our understanding of many basic tenets of biology.

The book is the product of the Second International Conference on the Monarch Butterfly ("Moncon-2"), held in September, 1986, at the Natural History Museum of Los Angeles County in California. The international make-up of the participants (from seven countries and four continents) is reflected in the contributions, which served to remind me that, although the Monarch has been proposed as the national insect of the United States, this butterfly does in fact have a very wide distribution and is an important component of the fauna of many parts of the world. The goal of the book, like the goal of the Conference, seems to be to bring together a variety of papers that exemplify the diversity of studies that have featured aspects of the biology of the Monarch butterfly. In that it was successful: the book is diverse in subject matter, represents many different perspectives, and encompasses many different fields of endeavor.

The book is divided into 10 sections: Introduction; Systematics; Chemical Communication; Mating Behavior; Hostplant Use, Cardenolide Sequestration, and Defense Against Natural Enemies; Physiological Ecology and the Annual Cycle; Migration; Overwintering Biology; Conservation; and Conclusions. Each section contains from one to nine chapters that range from short notes, to observational studies, to field and laboratory experiments.

These 10 sections cover three main themes: the chemical ecology of Monarchs, their hostplants, and natural enemies; migration and overwintering; and conservation.

The Introduction is just that; it introduces the various parts of the book and highlights the importance of the Monarch butterfly as a model system for studying many aspects of biology. The Systematics section contains only a single paper, but it is an important one. As the authors stress, it is only by putting the Monarch and its relatives into an appropriate evolutionary context that we can understand its fascinating biology. The section on Chemical Communication includes three papers that cover various aspects of the role of pheromones in courtship and reproduction on Monarchs and other danaines. The fourth section, on Mating Behavior, also contains three papers. Although these are also concerned with courtship and reproduction, they take a different perspective than the previous section, and emphasize the behaviors and population dynamics of reproduction in Monarch butterflies. The section on Hostplant Use, Cardenolides and Defense contains six chapters that cover various aspects of the hostplant-related chemical ecology of Monarchs. The section begins with a short but provocative chapter on the evolution of sequestrative ability in butterflies. This is followed by three well-done papers on the chemistry and dynamics of sequestration of cardenolides, a short paper indicating that members of the Apocynaceae (dogbanes) are not appropriate hostplants for Monarch larvae, and another in the series of thought-provoking papers showing that the Monarch-Queen-Viceroy mimicry complex is more complicated and more fascinating than originally conceived. Section 6, on Physiological Ecology, is a diverse set of four papers, three of which cover different aspects of physiology (endocrinology, thermoregulation), and the fourth, which seemed somewhat out of place, but was nonetheless interesting, covers the biology of Australian danaines.

Sections 7 and 8 treat Migration and Overwintering, respectively, and are where the bulk of the papers are concentrated. Nine chapters under Migration cover various aspects of migration biology in North and Central America, as well as Australia. Several of these papers address questions about the pattern of these migrations as well as their evolutionary origins. Related to these chapters are those of Section 8 on overwintering biology. These eight papers address more physiological areas of investigation as well as the interaction of Monarchs with predators.

Section 9 is concerned with the Conservation of the Monarch, especially the overwintering areas in California and Mexico. The eight papers in this section illustrate the importance of international cooperation and its potential for success in conservation of the Monarch and its remarkable migratory life history. The final section contains only a single, concluding paper, which does a good job of pulling together the wealth of information we are introduced to in this volume.

In reading over these chapters, it struck me that, in many of them, even as the authors describe how much we do know about the Monarch, they caution that there is still so much that we do not know. This was true of chapters in each of the sections. I view this as a call to biologists of every kind to continue and to expand their efforts in studying Monarch biology.

This book has many strengths. First, it pulls together workers from many disciplines (systematics and evolution, behavior, physiology, ecology, conservation) whose combined expertise gives a fairly complete picture of the biology of this remarkable insect. Second, the broad range of contributors and topics emphasizes how diverse the work on this particular butterfly has been, and highlights how much we have found out about it in the last 30 years. Third, despite how much we know, these contributions also show that much more needs to be done and the book gives some indication of where the focus needs to be. For example, surprisingly little is known about interactions of Monarchs and natural enemies in natural settings. Fourth, the emphasis on conservation issues is important, but also included is information on what is being done, in both the United States and Mexico, to preserve the overwintering sites of these butterflies. Fifth, some contributions raise controversial ideas that may change the way we think about the biology of the Monarch; for example, the Columbus hypothesis about the evolution of migratory ability and the idea that pyrrolizidine alkaloids may be as important as cardenolides in the chemical defense of some danaines.

The book also has some weaknesses. Perhaps most frustrating is the amount of time between the conference (1986) and the publication of the volume (1993). Another difficulty is that the quality of the chapters varies a great deal. Some chapters were very short, reporting on a small series of observations; whereas others reported results of detailed experiments or lengthy observations or were more synthetic in scope. Also, the book is expensive, which may prevent the wide readership that the book deserves (but there are always libraries).

The diversity of the book's coverage can be problematic but may also be a strength—there is something in it for everyone, from a student interested in conservation biology to a chemist interested in sequestration, to a person who just enjoys the biology of butterflies. Although this book is about the Monarch butterfly, it has articles and ideas with application to a variety of fields and areas of interest. One concern of mine is that the value to other fields will be lost because potential readers may judge from the title that it does not contain anything relevant to them. I would argue the opposite: that this book is valuable to biologists (and I use this term in the broadest sense, not just referring to professional biologists) in many areas of endeavor. I recommend it highly.

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NOCTUIDAE EUROPAEAE, VOLUME 1. NOCTUINAE I, by Michael Fibiger (English text with French translation in apposition). 1990. Entomological Press, Sorø, Denmark, 208 pp., 14 text figures, 16 color plates, 130 distribution maps. Hardcover, 23 × 29 cm, ISBN 87-89430-01-8. DKK680 (Danish kroner, about $125 exclusive of postage and bank charges).

NOCTUIDAE EUROPAEAE, VOLUME 2. NOCTUINAE II, by Michael Fibiger (English text with French translation in apposition). 1993. Entomological Press, Sorø, Denmark, 230 pp., 32 text figures (including line drawings and black-and-white photographs), 11 color plates, 116 distribution maps. Hardcover, 23 × 29 cm, ISBN 87-89430-02-6. DKK680 (Danish kroner, about $125 exclusive of postage and bank charges).

NOCTUIDAE EUROPAEAE, VOLUME 6. CUCULLIINAE I, by Gábor Ronkay and László Ronkay (English text with French translation in apposition). 1994. Entomological Press, Sorø, Denmark, 282 pp., 218 text figures, 10 color plates, 60 distribution maps. Hardcover, 23 × 29 cm, ISBN 87-89430-03-4. DKK680 (Danish kroner, about $125 exclusive of postage and bank charges).

NOCTUIDAE EUROPAEAE, VOLUME 7. CUCULLIINAE II, by Gábor Ronkay and László Ronkay (English text with French translation in apposition). 1995. Entomological Press, Sorø, Denmark, 224 pp., 182 text figures, 4 color plates, 55 distribution maps. Hardcover, 23 × 29 cm, ISBN 87-89430-04-2. DKK680 (Danish kroner, about $125 exclusive of postage and bank charges).

All volumes sold and distributed by Apollo Books, Lundbyvej 36, ADK-5700 Svendborg, Denmark; subscription to series provides 10% discount.

This impressive faunal series attempts a comprehensive assault on the classification, identification, and distribution of European moths in the family Noctuidae. The first four volumes of the series, covering only the subfamilies Noctuinae and Cuculliinae, contain treatments for 368 species in 69 genera. Despite centuries of taxonomic work on the European fauna, these volumes contain descriptions for 2 genera, 4 species, and 21 subspecies that are new to science. Taxonomic action abounds, with resurrection of 2 generic

names, changes in status for 51 species-group names, and new synonymies for 104 species-group names and 3 genera!

All volumes are attractively and securely bound with pale gray covers, the spine lettering giving series and volume titles in bold black. Layout of the text throughout is in two parallel columns, the left in English and the right in French. Format, choice and variation of fonts, and integration of text with range maps is attractive and convenient. Volume 1 has a small number of incorrect spellings in the text, including at one point the author's own name, with occasional confusion between 'synonomy' and synonymy. The other volumes appear quite free of errors.

The presswork is exceptional, the text on glossy white paper of neutral pH, and the color plates on matte paper with high resolution and excellent rendition, much better than plates in earlier fascicles of the *Moths of America North of Mexico* series well known to American readers, and competitive with plates in more recent fascicles in that series. With few exceptions the specimens illustrated are in excellent condition, well prepared, and photographed *en masse* against a pale gray background without shadows, effectively contrasting with white or luteous wing margins. Plate captions bear full label data and repository information for all specimens.

In general, the series exhibits taxonomic rigor, including resolution of available type material, careful and detailed diagnoses, and extensive coverage of nomenclature. Species-group synonyms are regrettably listed without original generic combinations, but authors' names and year of publication provide citations to all original descriptions by way of the complete list of references at the end of each volume. Coverage is impressive for available names, as well as infrasubspecific ones, and includes many names not found in R. W. Poole's *Lepidopterorum Catalogus (New Series), Fascicle 118, Noctuidae* (1989, E. J. Brill/Flora and Fauna Publications, New York). For instance, all six synonyms listed for *Mesogona oxalina* are missing from Poole's compendium.

Recent proliferation of diverse notions concerning the phylogeny of Noctuidae has presented special problems for this serial publication, as have changes in the political boundaries of eastern Europe. Confusion over delimitation of genera, tribes, and subfamilies in the recent literature is rivalled only by readers' confusion over the political boundaries of the countries they inhabit, especially in eastern Europe.

The work suffers from the absence of any meaningful discussion on the classification of the family as a whole. Only a single paragraph introduces the family in Volume 1, and there are no keys to subfamilies or tribes in any volume. Evolutionary discussions are brief in volumes 1 and 2, largely limited to expressing confusion over how the sequence of appearance in the text should reflect concepts such as "most advanced" or "most primitive." Volume 1 offers no reference to J. D. Lafontaine's outline of evolutionary trends in the speciose genus *Euxoa* (1987, *Noctuoidea. Noctuidae (Part). Noctuinae (Part—Euxoa), Moths of America North of Mexico, Fascicle 27.2,* The Wedge Entomological Foundation, Washington, D.C.) based on features of the genitalia of both sexes, although speculation is offered on phylogenetic trends for some male features (harpe, sacculus, vesica). Expressions such as "[*Pleonectopoda* is] the second most primitive European subgenus" are quite mystical, as no clear phylogeny is postulated or discussed. Additional information on the phylogeny of the subfamily Noctuinae is promised in the still unpublished Volume 3. The absence of phylogenetic information in the early volumes contrasts sharply with similar introductions in other faunistic works e.g., Lafontaine (1987, *op. cit.*) for the subfamily Noctuinae, or E. Berio (1985, *Fauna d'Italia, Lepidoptera, Noctuidae. I. Generalità, Hadeninae, Cucullinae [sic],* Edizioni Caliderini, Bologna) for the family.

Species accounts are broken into sections, including Taxonomic Notes, Diagnosis, Bionomics, Distribution, and Remarks. The sections entitled Taxonomic Notes are usually detailed, often providing comparative information useful for identification. The diagnoses are clear for each species, and are provided for each subspecies whenever trinomens are applied. In many cases for close species the diagnoses are incisive and useful, emphasizing subtleties of maculation, antennae, and size. Volumes 1 and 2 (Noctuinae) are relatively weak on genitalic information, but Volumes 6 and 7 (Cuculliinae) contain detailed description and illustration of genitalia where appropriate. In a few cases "differences in

genitalia" are referred to, but the actual structures are not, leaving readers to unravel those features for themselves.

The Bionomics sections are informative, elaborating on habitats, dominant vegetation, phenology, daily adult activity cycles, and, in some cases, resting postures and feeding habits of both adults and larvae. Foodplants are identified with scientific names whenever possible.

The geographic area of coverage extends from Iceland and the Azores to the Ural Mountains, but does not include Turkey, Cyprus, the Middle East or Northern Africa. A single standard base map depicting political boundaries for the entirety of Europe is used in all volumes to illustrate ranges for each species. The maps are not numbered, labelled only with a binomen, and are not cited in the text. Subspecies are not mapped separately and maps for species do not distinguish the presumably allopatric or parapatric distribution of subspecies. Distributions are presented as areas bounded by a thick line and shaded with broad stripes through which political boundaries within the range remain clearly visible. Ranges are stated to be schematic representations of more precise maps produced by a project entitled "*Faunistica Lepidopterorum Europaeorum.*" In fact, the shaded areas are quite generalized, leaving the reader with a feeling of uncertainty as to how literally one might interpret occurrence based solely on them.

The References section at the end of each volume is very complete and inclusive, but regrettably all periodical titles are abbreviated, making obscure references difficult to locate for readers without bibliographic experience or a friendly librarian. Indices wisely include names of the genus group as well as those of the species group, but in Volumes 1 and 2 no explanation is offered for the use of semibold page numbers to locate principal treatments. Indices for Volumes 6 and 7 correct this problem and add figure numbers for genitalia. Plate numbers are not included in the indices, and readers are forced to look up the species account in order to obtain plate citations. Unfortunately no index to foodplants is provided, and common names are not mentioned. Both features would have broadened the appeal of the series, and more importantly, increased its utility as a reference work for use by non-specialists.

Genitalia are illustrated for only a few species in Volumes 1 and 2. Although citations for genitalia illustrations in other publications are given for many species, and a comprehensive set of illustrations is promised in a still unpublished Volume 3, the situation is frustrating for users who desire genitalic confirmation and have no access to other literature. Volumes 6 and 7 correct this problem with complete illustration of the genitalia for both sexes. These are accurate tracings of actual preparations reproduced at large size, only one or two per page, but in detail and presentation are not up to the illustration standards of other faunistic works.

VOLUME 1 primarily covers the Agrotini of Lafontaine (1987), and treats 137 species in 16 genera including prodigious assemblages in *Euxoa* and *Agrotis.* Systematically difficult taxa in *Dichagyris* and *Yigoga* (= *Ogygia* of Hübner) are treated in detail, complicated by the faunistic nature of the series which prevents thorough treatment of extralimital taxa for these Palearctic lineages.

Discussion of the *Hypericum*-feeding genus *Actinotia* in Volume 1 is informative, but the evidence presented makes its retention in Volume 1 enigmatic. American readers will wonder why the closely related New World genus *Nedra* is not mentioned, as the two genera are classic examples of how excessive adherence to single Hampsonian features (in this case tibial spinulation) can result in preposterous subfamilial placement of closely related lineages. Equally confusing, but less resolved, is the inclusion of the single European species of *Axylia.*

New World readers will recognize the distinctive flame-shouldered dart (*Ochropleura plecta*) in the plates. The genus *Ochropleura* is considered to be a basal lineage of Noctuini by Lafontaine (1987). Its generic limits are very broadly construed in Volume 1, although paraphyly of that grouping is acknowledged.

Two new species and nine subspecies are described in the main text of Volume 1, with authorship diversely credited to Fibiger, Moberg and Fibiger, or Fibiger and Moberg. All possible combinatorials in nomenclature are nearly attained in the Appendix, where an extralimital species, *Euxoa mobergi* Fibiger, is described!

VOLUME 2 treats 116 species in 27 genera, primarily those placed in Noctuini of Lafontaine (1987), but including *Peridroma,* a genus Lafontaine considered to be a basal lineage of Agrotini. Fibiger proposes one new genus, *Divaena,* and two other genera are resurrected from synonymy. Fifty-one species-group names are pronounced as new synonyms, and 14 undergo revisions in status. Six new subspecies are described. Volume 2, in contrast to Volume 1, benefits greatly from Fibiger's active communication with other specialists, especially with the world doyen of noctuine systematists, J. D. Lafontaine, who provides critical information on delimitation of many genera, including *Epipsilia, Rhyacia, Cyrebia, Protolampra, Eugraphe,* and *Coenophila,* as well as advice on relationships of *Peridroma* and the classification of the *Xestia* complex. American readers will appreciate illustration of two showy species recently introduced into North America, *Noctua pronuba* and *N. comes,* and will notice that North American *Xestia* (*Megasema*) *adela* Franclemont is considered a subspecies of *X. c-nigrum* (Linnaeus), with *X. dolosa* Franclemont treated as a distinct species.

The genus *Mesogona* is admittedly misplaced in Volume 2, but retained because it was included in the plates prior to recognition of its relationship to *Enargia, Cosmia, Ipimorpha,* and other genera historically placed in a polyphyletic Amphipyrinae or more recently in Ipimorphinae by European workers. A corrigenda in Volume 2 provides input from various active European specialists on errors of omission and commission in Volume 1.

Unlike Volumes 1 and 2 by Fibiger, Volumes 6 and 7 by Ronkay and Ronkay attempt to provide phylogenetic clarification for the lineage under discussion, the Cuculliinae. This subfamily is considered by them to contain five tribes of uncertain relationship, including Cuculliini (*Cucullia* and kin), Oncocnemidini, Psaphidini, Feraliini, and Episemini. Their phylogenetic conclusions are similar to those of R. W. Poole (1995, *Noctuoidea. Noctuidae (Part). Cucullinae, Stiriinae, Psaphidinae (Part), Moths of America North of Mexico, Fascicle 26.1,* The Wedge Entomological Foundation, Washington, D.C.) for the Nearctic fauna, although Poole treats the lineages as subfamilies (Cuculliinae, Oncocnemidinae, and Psaphidinae with Feraliini as one of six Nearctic tribes). Nomenclature enthusiasts will enjoy figuring out senior authorship for the flurry of family-group names being proposed, but phylogeneticists may conclude little with confidence as extensive comparative analyses have not yet been made, especially for pupal and larval structures that might clarify parallel trends observed in adults features, especially genitalia. Both works will introduce non-specialists to new subfamily classifications for trifine noctuids that contrast sharply with the traditional system in use for nearly a century based on Hampson's classic *Catalogue of the Lepidoptera Phalaenae in the British Museum* (1903–1913). Even novices will note the disappearance of *Lithophane, Eupsilia, Xylena,* and related genera of pinion and sallow moths from the "new" Cuculliinae, leaving only *Cucullia* and close kin, with the predominantly eremic oncocnemidines as a likely sister group. Relationship of the weaker-tongued sallow moths such as species of *Feralia, Brachionycha, Asteroscopus,* and *Lamprosticta* are much less convincing, but together they may constitute a lineage including Nearctic *Psaphida.*

VOLUME 6 begins with a comprehensive and fully revised checklist of the tribe Cuculliini for the Palearctic Region. Species accounts are provided for the entirety of the European fauna consisting of 60 species in just three genera, *Cucullia* (sensu stricto), its segregate *Shargacucullia,* and the monotypic *Calocucullia.* The former two genera are each divided into several species groups. Poole (1995) agrees that *Shargacucullia* may be monophyletic, but aptly questions the wisdom of separating it from *Cucullia* (s.s.) as together they comprise the long accepted and undoubtedly monophyletic genus *Cucullia* (sensu lato). Species accounts in Volume 6 are detailed and the diagnoses extensive, giving an impression of thoroughness, precision, and much thought by the authors. One new species and one new subspecies are proposed in Volume 6; 11 species-group names are given revised status, and six names are newly treated as synonyms.

VOLUME 7 contains treatments for 23 genera and 55 species, covering European relatives of cuculliine taxa placed by Poole (1995) in the Oncocnemidinae. One new genus and five new subspecies are proposed; three generic names and four species-group names are newly synonymized, and an additional 16 names undergo changes in status. As in Volume 6, species treatments in Volume 7 are quite thorough, with detailed discussion

and illustration of the genitalia of both sexes. The Bionomics sections are full of detail, including larval foodplants and comments on activity periods during the night reflecting the authors' substantial field experience.

The lineages covered in Volume 7 have their greatest diversity in the New World, and clear understanding of relationships must await revision of the extensive Nearctic fauna as well as resolution of enigmatic taxa from the southern neotropics. *Calophasia lunula*, a recent introduction to North America feeding on both alien and native species of *Linaria*, is stated to be holarctic without clarification of its history in the Nearctic.

Volume 7 does have some confusing problems in organization, such as Plate 4 and its caption on page 144 appearing before the conclusion of the caption for Plate 3 on page 145, or the 76 pages of plates and figures (pp. 136–211) separating the main text from its last four pages.

Funding permitting, additional volumes of *Noctuidae Europaeae* will soon appear. If these continue to improve in response to modern analyses of phylogeny while maintaining the current high quality of the published volumes, the series will become the most impressive regional fauna in existence for any family of moths. Encyclopedic coverage of the regional fauna, combined with superb color illustrations of adults and a comprehensive concatenation of literature and personal communications from world specialists, have already made this series a truly magistral contribution on the Noctuidae of Europe.

JOHN E. RAWLINS, *Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080.*

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CORRECTION TO VOLUME 50

In the article by George Austin, "Hesperiidae of central Rondônia Brazil: three new species of *Narcosius*" which appeared in 50(1):54–60, the adults on page 56 are numbered incorrectly. The caption should read: "FIGS. 1–4. **1.** *Narcosius steinhauseri,* holotype male. **2.** *Narcosius odysseus,* holotype male. **3.** *Narcosius pseudomura,* holotype male. **4.** *Narcosius mura,* male (BRAZIL: Rondônia; 62 km S Ariquemes, linea C-20, 7 km E B-65, Fazenda Rancho Grande). On all figures, venter on left, dorsum on right." Similarly, on page 55, "(Figs. 3, 8)" should appear under *Narcosius pseudomura*; on page 57, under Diagnosis and Discussion, *Narcosius mura* should be noted as illustrated in "(Fig. 4);" and on page 57, "(Figs. 2, 6)" should appear under *Narcosius odysseus.*

Date of Issue (Vol. 50, No. 2): 5 July 1996

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11 October 1996

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GENITALIA AND THE PROPER GENUS: *CODATRACTUS* GETS *MYSIE* AND *UVYDIXA*—IN A COMPACT *CYDA* GROUP—AS WELL AS A *HYSTER*ECTOMY, WHILE *CEPHISE* GETS PART OF *POLYTHRIX* (HESPERIIDAE: PYRGINAE)

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ABSTRACT. Many features of genitalic morphology show that Evans's monotypic, neotropical genus *Cephise* contains not only additional tailless species but also several species with long hindwing tails currently misplaced in the unrelated genus *Polythrix*: *Cephise auginulus* (Godman & Salvin), **new combination**, *Cephise callias* (Mabille), **new combination**, and *Cephise guatemalaensis* (Freeman), **new combination**. (Even with their removal, *Polythrix* is still polyphyletic.) There are major problems with the names of various tailed and tailless species of *Cephise*. All species of *Cephise* express a remarkable character state of the palpus (males more fully than females) in which scales at the distal end of the first segment turn sharply outward across the ventral edge of the eye. In Guanacaste, Costa Rica, larvae of both a tailless species (***Cephise nuspesez*, new species**) and a tailed species (*C. auginulus*) eat the same plants: 4 species in the Malpighiaceae and 1 in the Combretaceae. Both tailed and tailless species are widespread, collectively ranging from San Luis Potosí, Mexico, to Bolivia, Paraguay, northern Argentina, and Brazil.

Again, features of genitalic morphology serve in extracting species from disparate genera (*Thorybes*, *Cogia*) (and from synonymy) and uniting them with *Codatractus cyda* (Godman) in a compact species group. Like *cyda*, the added species—*Codatractus mysie* (Dyar), **new combination**, and *Codatractus uvydixa* (Dyar), **new combination**—are tailless; but some species of *Codatractus* are prominently tailed. The three species of the *cyda* group closely replace one another geographically, from southeastern Arizona to northwestern Honduras; their distribution strongly reflects allopatric speciation and reinforces their taxonomic union. In superficial appearance, the geographically intermediate (strictly Mexican) species, *uvydixa*, resembles the southeastern *cyda* in Chiapas, Puebla, and Guerrero, but the northwestern *mysie* in Colima, Jalisco, and Sinaloa. Although all three species are genitalically extremely close, they differ markedly in size (*mysie*, smallest; *uvydixa*, largest); and *mysie* differs completely from *uvydixa* and *cyda* in the number of segments in the nudum of the antenna—an unusual evolutionary development for closely related species.

Removed from *Codatractus* on morphologic (and also behavioral) grounds, *hyster* (Dyar) is temporarily a species **incertae sedis**.

Additional key words: allopatric speciation, Combretaceae, Malpighiaceae, New World, palpus.

Species in the wrong genus can mask, warp, or wreck potential insights. It takes properly delimited groups to make valid evolutionary patterns.

Closely related species often replace one another geographically. This evolutionary pattern has been so thoroughly documented that now, when species thought to be closely related on morphologic grounds turn out to be closely allopatric, the distribution can be viewed as independent evidence for their close relationship. I adopt such a semicircular view later in this paper.

Congeneric species tend to have essentially similar copulatory parts. Again, this evolutionary pattern has been sufficiently well supported that one can fairly reverse it by pulling genitalically similar species together and saying they are related.

With a primary interest in nearctic skippers, I have lately been emphasizing genitalic morphology in changing the limits of many much-used, much-studied, long-stable, and supposedly well-defined genera (Burns 1987, 1989, 1990, 1992, 1994a, 1994b). My revisions have variously involved generic lumping, generic splitting, and especially the shifting of species from one genus to another (or to temporary limbo, when they screamed for release without telling me where they should go). I have pursued the genera in question throughout their geographic ranges, which has usually led from the nearctic to the neotropics (but occasionally to the palearctic). Though the genera treated so far (*Hesperia, Atalopedes, Polites* [incorporating both *Poanopsis* and *Yvretta*], *Atrytone, Anatrytone* [assuming its own identity], *Paratrytone, Poanes, Ochlodes, Quasimellana* [superseding *Mellana*], and *Amblyscirtes*) are all hesperiine, hesperiines have no monopoly on the taxonomic mess.

The pyrgine genus *Codatractus* (which enters the United States in southern Texas, New Mexico, and Arizona, and extends to northern Argentina) first intrigued me because it included both prominently tailed (e.g., Figs. 89, 90) and totally tailless (e.g., Figs. 85–88) species. Morphologic comparison of these species, with particular attention to genitalia, shows that all but one really do belong in a single genus. It follows that striking differences in wingshape can evolve with relative ease.

Variations on the tailed-and-tailless pattern appear in other pyrgine genera such as *Thessia*, which Steinhauser (1989) proposed for two species (with peculiar, and notably similar, male and female genitalia) that Evans (1952) stuck in *Urbanus* and *Achalarus*: *Thessia athesis* (Hewitson) has hindwings with short but definite tails whereas *T. jalapus* (Plötz) has hindwings with slight lobes. *Thessia* ranges from the United States (southern Texas) to Colombia and Venezuela, plus Tobago (Evans 1952).

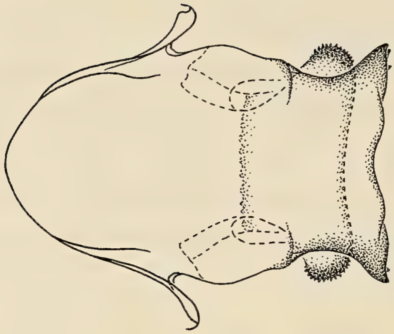
As currently constituted, the genus *Typhedanus* includes five species with long hindwing tails and six without (Evans 1952, Freeman 1977, Mielke 1979). *Typhedanus* ranges from the United States (southern Texas) to central Argentina (Hayward 1948).

CEPHISE

The genus *Cephise* embraces species with long hindwing tails as well as species with strong hindwing lobes (Figs. 28–51)—but not as currently constituted. Evans (1952:136, 153) proposed *Cephise* (in his *Celaenorrhinus* group of genera, with the admonition "systematic position . . . doubtful") for what he considered the single species *cephise* (Herrich-Schäffer), comprising two genitalically differentiated subspecies, *cephise* and *hydarnes* (Mabille); and he listed several synonyms under these names. In reality, Evans's *Cephise* is a complex of species, ranging from at least as far north as San Luis Potosí, Mexico (Freeman 1970), to Peru, Paraguay, and Misiones, Argentina (Hayward 1948), with hindwings that are "strongly lobed at [the] tornus" (Evans 1952:136).

Evans (1952:67) called *Polythrix* "a compact genus in respect of general appearance, characterised by the spot in space 3 of the forewing being approximate to the central spots and the apical spots being in a straight line. Hindwing elongate with a long tail." But appearances can be deceiving. Like other genera in his *Urbanus* group (and elsewhere), *Polythrix* is polyphyletic, partly because two of the thirteen species Evans included are long-tailed species of *Cephise*: *Cephise auginulus* (Godman & Salvin), **new combination** (Figs. 40–43) (see next paragraph), and *Cephise callias* (Mabille), **new combination**. A *Polythrix* later described by Freeman (1977) is yet another tailed *Cephise*: *Cephise guatemalaensis* (Freeman), **new combination** (Figs. 48–51). (However, *Polythrix kanshul* Shuey, recently described from southern Mexico and central Panama, is a true *Polythrix* because [a] Shuey [1991] showed, with genitalic characters, that *kanshul* forms a monophyletic lineage with *P. metallescens* [Mabille] as well as *P. eudoxus* [Stoll] and [b] *metallescens* is the type of *Polythrix*.) Like their tailless counterparts, the tailed species of *Cephise* collectively span most of the neotropics from San Luis Potosí and Veracruz, Mexico, to at least Brazil (Plötz 1881) and Bolivia (Evans 1952).

I am resurrecting the name *auginulus*, which Evans (1952:70) listed with *aelius* Plötz and *callicina* Schaus as synonyms of *Polythrix procerus* (Plötz), because I doubt that *auginulus* and *procerus* are the same. Although the precise identity of *procerus* eludes me, that of *auginulus* does not: Godman and Salvin (1893), in describing *auginulus* from two males from Mexico (Veracruz) and Guatemala (type locality), provided a good figure of the genitalia (vol. 3, pl. 75, fig. 22), along with color figures of the dorsal and ventral surfaces of the whole animal. Godman (1907) stated, after examining Plötz's unpublished color figures of American skipper species, that neither *procerus* nor *aelius* (each described by



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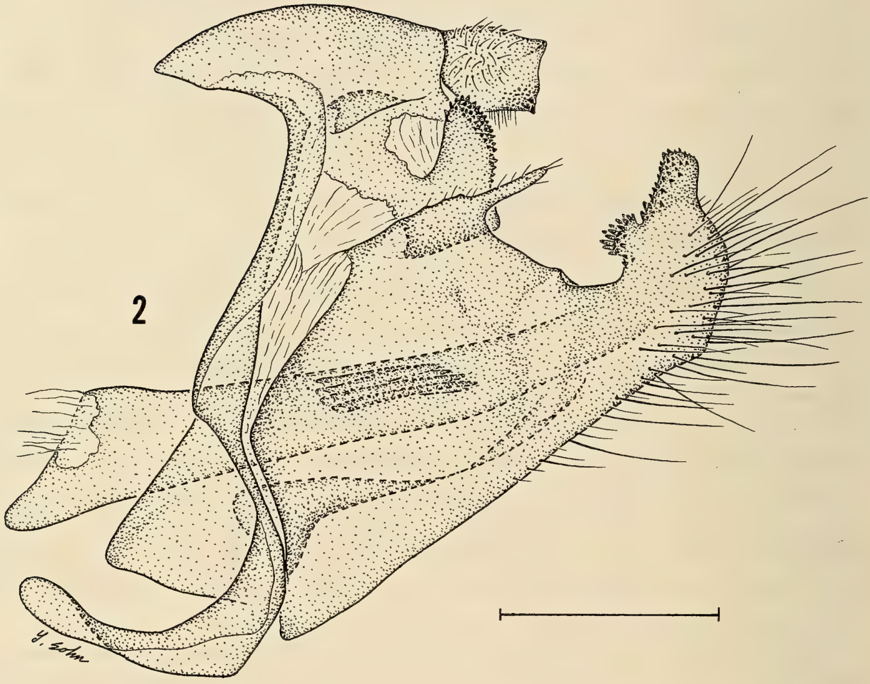

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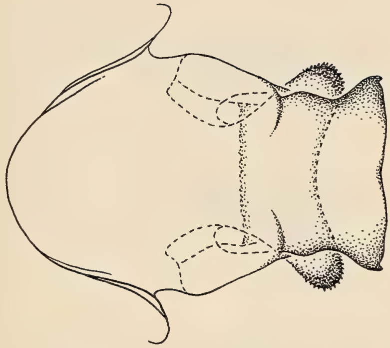
FIGS. 1, 2. Male genitalia of *Cephise hydarnes* (sensu Hayward 1948 and Evans 1952) from PARAGUAY (J. M. Burns genitalic dissection no. X-1400) (USNM). Scale=1.0 mm. **1,** Tegumen, uncus, and gnathos in dorsal view. **2,** Complete genitalia (minus right valva, which is not entirely symmetrical with the left valva), with vesica retracted and cornuti bundled, in left lateral view.

Plötz from Pará) was in the Godman and Salvin collection. In other words, these Brazilian skippers did not look to Godman exactly like his Mexican/Guatemalan *auginulus*. From my perusal of the original descriptions of *procerus* and *aelius* (Plötz 1881), I suspect that these skip-



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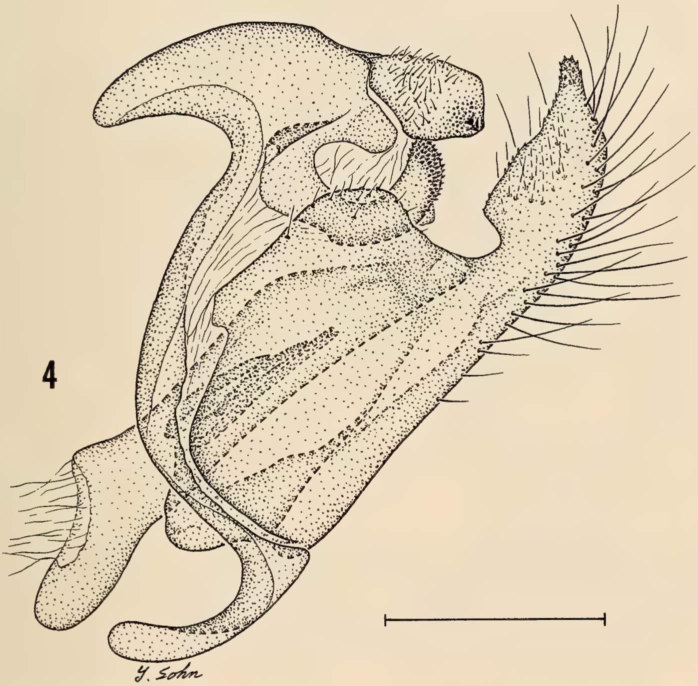

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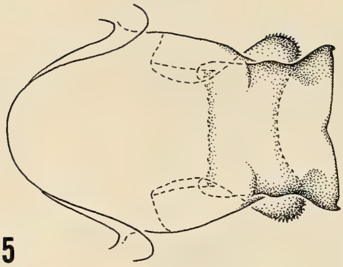
FIGS. 3, 4. Male genitalia of *Cephise orima* (holotype of *Nascus orima* Schaus) from Petrópolis, BRAZIL (X-1401) (USNM). Scale=1.0 mm. **3,** Tegumen, uncus, and gnathos in dorsal view. **4,** Complete genitalia (minus right valva), with vesica retracted and cornuti bundled, in left lateral view.

pers differ not only from *auginulus* but also from each other. For years I have mistrusted Evans's synonymies. Now, having clearly shown (Burns 1994b) that the four synonyms listed by Evans (1955) under *Mellana clavus* Erichson are four separate species (in two different species groups) of *Anatrytone* and that *clavus* itself is a species of *Wallengrenia*,



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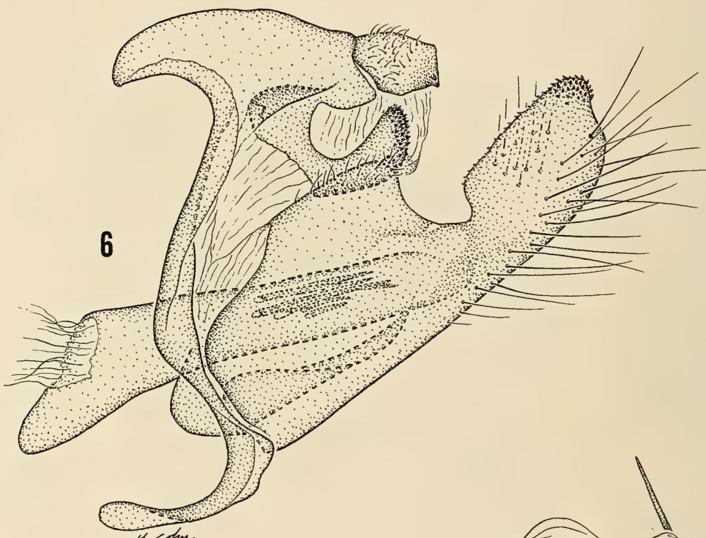

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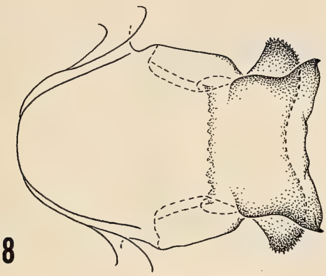
FIGS. 5–7. Male genitalia of *Cephise nuspesez* from the Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (USNM). Scale=1.0 mm. **5,** Tegumen, uncus, and gnathos in dorsal view (holotype, Santa Rosa Sector, rearing voucher 81-SRNP-646, dissection X-1345). **6,** Complete genitalia (minus right valva), with vesica retracted and cornuti bundled, in left lateral view (holotype, Santa Rosa Sector, rearing voucher 81-SRNP-646, dissection X-1345). **7,** Aedeagus, with vesica everted and cornuti splayed, in dorsal view (paratype, Guanacaste Sector, rearing voucher 91-SRNP-2079, dissection X-3735).



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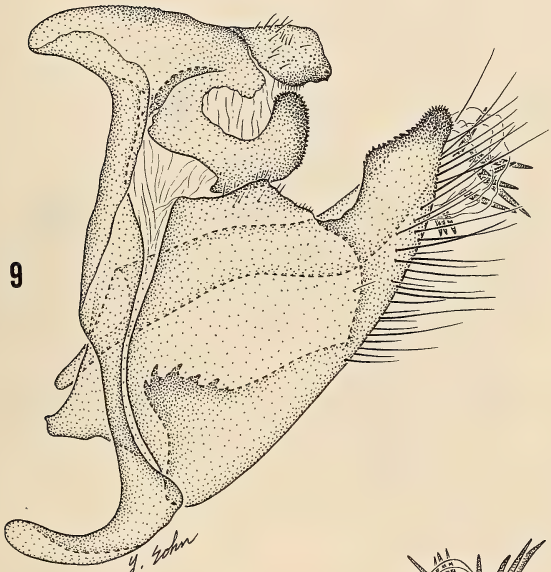

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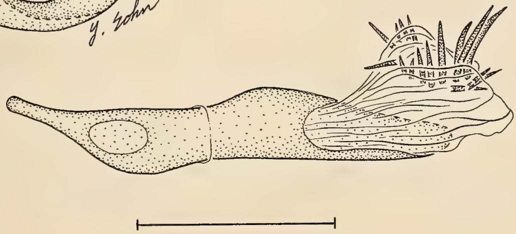

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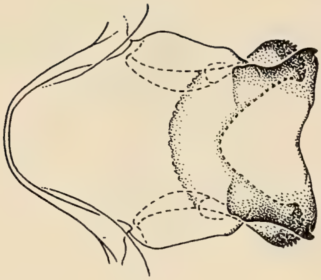
FIGS. 8–10. Male genitalia of *Cephise auginulus* from the Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 92-SRNP-3959, dissection X-3828) (USNM). Scale=1.0 mm. **8,** Tegumen, uncus, and gnathos in dorsal view. **9,** Complete genitalia (minus right valva), with vesica everted and cornuti splayed, in left lateral view. **10,** Aedeagus, with vesica everted and cornuti splayed, in dorsal view.



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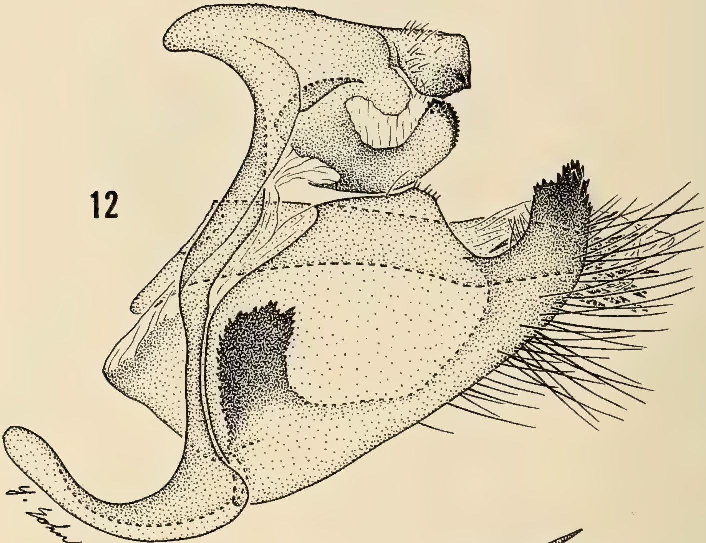

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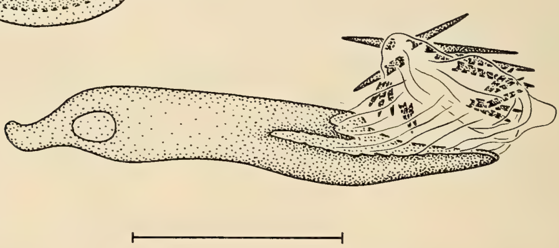

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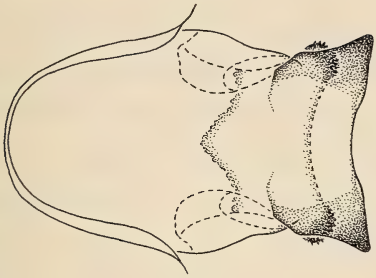
FIGS. 11–13. Male genitalia of *Cephise* nr. *callias* from Saül, 200–450 m, 3°37' N, 53°43' W, FRENCH GUIANA, 16 November 1993, D. J. Harvey (X-3900) (USNM). Scale=1.0 mm. **11,** Tegumen, uncus, and gnathos in dorsal view. **12,** Complete genitalia (minus right valva), with vesica everted and cornuti splayed, in left lateral view. **13,** Aedeagus, with vesica everted and cornuti splayed, in dorsal view.



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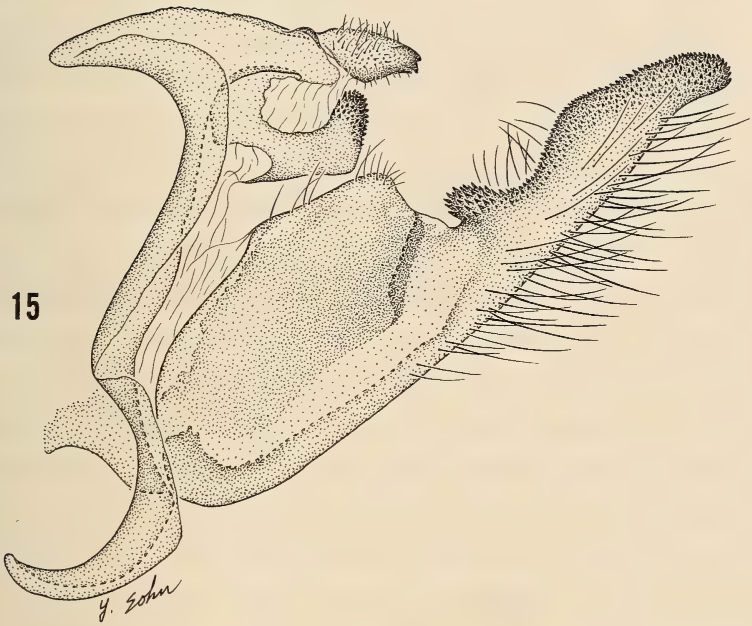

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FIGS. 14–16. Male genitalia of *Cephise guatemalaensis* (holotype of *Polythrix guatemalaensis* Freeman) from Sayaxché, Petén, GUATEMALA, 23 August 1963, E. C. Welling (Freeman genitalic dissection no. H-674) (AMNH). Scale=1.0 mm. **14,** Tegumen, uncus, and gnathos in dorsal view (split in uncus plus adjacent tegumen, and torn perimeter of tegumen, repaired). **15,** Genitalia (minus right valva, aedeagus, and portions of juxta) in left lateral view. (Repair includes reassembly and additions to the missing, inner, anteroventral corner of the left valva working from what remains in the corresponding position on the right valva [which may not be everything as it, too, is damaged].) **16,** Aedeagus, with vesica retracted and cornuti bundled, in dorsal view.

I am more skeptical than ever. I have examined the holotype of *Eudamus callicina* which Schaus (1902:425) described from a lone female from Honduras, with the comment "closely allied to *E. callias* Mabille." His comment is correct since *callicina* (Figs. 38, 39) is the same as *auginulus* (Figs. 40–43)—and a junior synonym of it.

The genitalia of *Cephise* exhibit a basic pattern in each sex. Most notable in males is the truncate uncus, with two or three small teeth at each posterolateral corner (Figs. 1–6, 8, 9, 11, 12, 14, 15). On either side of the uncus, the underlying, undivided gnathos sends up a thumb-shaped projection that is densely and finely dentate distally and posteriorly (Figs. 1–6, 8, 9, 11, 12, 14, 15). Because the many, tiny, close-set gnathosteeth are both conical and short, they create a nubbly surface. At rest within the aedeagus, the cornuti suggest a bundle of spines (Figs. 2, 4, 6, 16); but when the vesica everts, the cornuti dissociate in a stunning burst of spines (Figs. 7, 10, 13). In lateral view, the valva presents a large proximal end, followed by a more or less **U**-shaped notch and a ventrodistal extension that is finely to coarsely dentate dorsally and distally (Figs. 2, 4, 6, 9, 12, 15). The anteroventral, innermost edge of the valva extends more or less broadly and bluntly dorsad (Figs. 2, 4, 6, 9, 12, 15).

In females, heavy sclerotization around the ostium bursae and the caudalmost part of the ductus bursae is essentially **Y**-shaped in ventral view (Figs. 17, 18, 20–22). Arising from the sides of the sterigma and flanking the **Y** are paired, heavily sclerotized, ventromedially directed, and more or less serrate to pointed plates, which usually look wicked (Figs. 17–22). The top of the **Y** forms a funneling entryway, while the stem of the **Y** constitutes the beginning of the ductus bursae proper. Here the ductus bursae is midventral in position and narrow in diameter; the sclerotization (i.e., the stem of the **Y**) is limited, abruptly switching to membrane; and even the short, sclerotized **Y**-stem is unsclerotized in a dorsal, longitudinal strip (Figs. 17–22). Anteriad, the membranous ductus bursae angles at least slightly to the left and increases at least slightly in diameter (Figs. 17, 18, 20–22); and (with one known exception) a sizable, well-sclerotized piece wraps around it without completely encircling it (Figs. 17–21). (In the maverick species, the sclerotization, though still sizable, is light [Fig. 22]; and it is divided longitudinally into two separate, flanking strips instead of the single wraparound.) The corpus bursae is wholly membranous.

Immediately dorsad of the entire sterigma is a single, distinctive sac with an elaborately crinkled surface somewhat like that of the longer, paired sacs extending anteriad of the sterigma in females of such genera as *Proteides*, *Aguna*, *Codatractus*, *Urbanus*, *Astraptes*, *Calliades*, *Autochton*, *Thessia*, *Achalarus*, *Thorybes*, and *Cabares*. The anterior apophyses are rudimentary or absent while the posterior apophyses are

short, delicate, and, in lateral view, bowed ventrad (Fig. 19). On the paired ovipositor lobes, setae near the midventral line are shorter, sparser, and more delicate than peripheral setae, which are not only longer, denser, and more robust, but also directed outward and backward (Fig. 17), imparting a sort of saintly radiance in an aedeagal-eye view. No major setae are directed inward, toward each other, from the inner, ventral edges of the ovipositor lobes as they often are in *Urbanus* group females (Fig. 23).

The preceding generic characterization is distilled from genitalic dissections of 23 males in 7 species and 17 females in 6 species.

As you would predict, the skippers sharing this genitalic pattern have more than that in common. The palpi of *Cephise* are remarkable. At the distal end of the first segment, some of the scales that tightly clothe the palpus turn sharply outward across the ventral edge of the eye. Magnified, and seen from below, this projection of scales resembles a shelf nearly perpendicular to the body of the palpus (Figs. 24, 26); from in front, it looks like a triangle beneath the eye (Figs. 25, 27), often conspicuous because the exposed inner sides of the turned out scales tend to be paler than the outer sides of most other visible palpal scales (Fig. 27). Dark hairs always extend beyond the pale, turned out, shingle-like scales and usually curve ventrad (Figs. 24–27). Males express this peculiar projection of palpal scales more fully than do females. In either sex, it is more obvious in reared than in wild-caught specimens, owing to the wear and tear of skipper living.

Males of *Cephise* have a well-developed costal fold (Figs. 28, 32, 34, 40, 44, 48). They also have wonderfully furry metathoracic legs with wide rows of long hairs: down the femur, one row of less dense, paler hairs that tend to curl at the tips; and down the tibia, two rows of denser, darker hairs that tend to stay straight. These are not the same as the metatibial tufts of many and various pyrgine skippers.

The total number of nudum segments in *Cephise* ranges from 21 to 26 (usually 23, 24, or 25), with only 4 to 6 (usually 5 or 6) of the segments on the basal part of the antennal club before the apiculus (Table 1). The apiculus is about as long as, and decidedly more slender than, the basal part of the club and is sharply reflexed. Because—as in so many skippers—it is often not entirely clear where the basal part ends and the bent back apiculus begins, a line of demarcation between them (à la nudum counts of Evans) is somewhat arbitrary. I counted nudum segments in 100 specimens.

Instead of the monotypic genus that Evans (1952) envisioned, *Cephise* is a polytypic genus that may ultimately include as many as a dozen species, rather evenly divided between tailed and tailless. As I indicated in resurrecting *auginulus* for one of the tailed species, it is hard

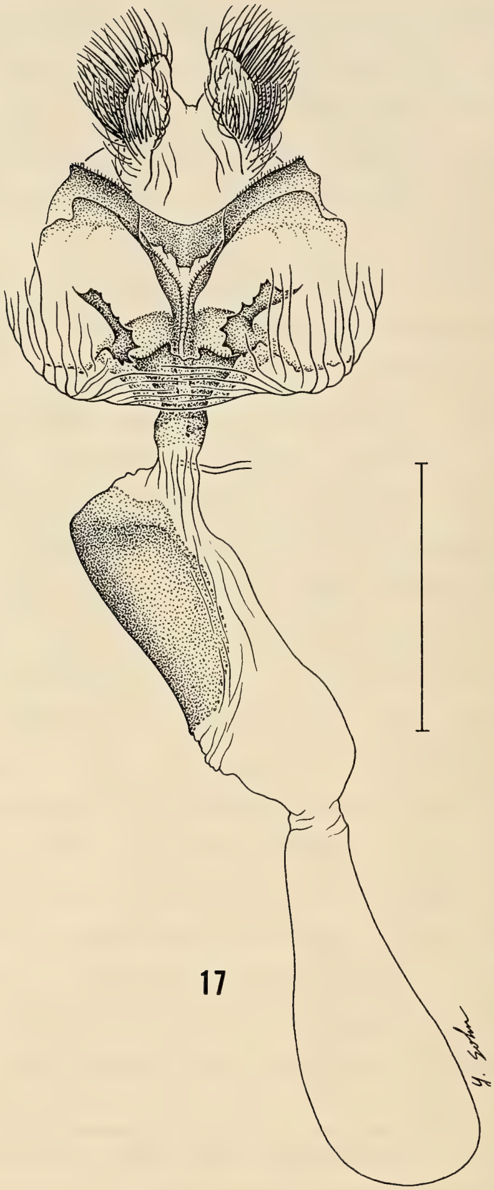

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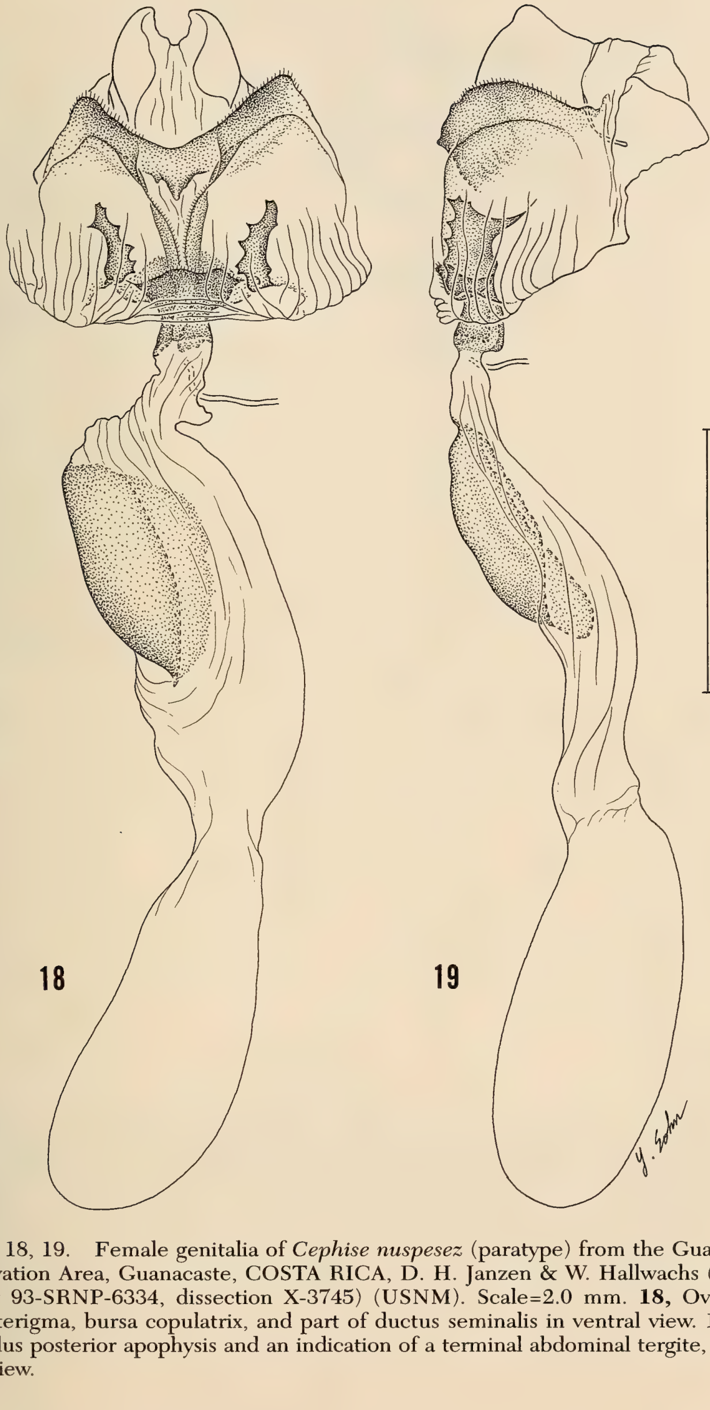
FIG. 17. Female genitalia of *Cephise orita* (holotype of *Nascus orita* Schaus) supposedly from PERU but probably from BOLIVIA (X-3885) (USNM). Ovipositor lobes (with an indication of their setae), sterigma, bursa copulatrix, and part of ductus seminalis in ventral view. Scale=2.0 mm.



FIGS. 18, 19. Female genitalia of *Cephise nuspesez* (paratype) from the Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 93-SRNP-6334, dissection X-3745) (USNM). Scale=2.0 mm. **18,** Ovipositor lobes, sterigma, bursa copulatrix, and part of ductus seminalis in ventral view. **19,** The same, plus posterior apophysis and an indication of a terminal abdominal tergite, in right lateral view.

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FIGS. 20, 21. Female genitalia of two species of *Cephise*. Ovipositor lobes, sterigma, bursa copulatrix, and part of ductus seminalis in ventral view. Scale=2.0 mm. **20,** *Cephise auginulus* (holotype of *Eudamus callicina* Schaus) from HONDURAS (X-3884) (USNM). **21,** *Cephise* nr. *callias* from Paraíso, Canal Zone, PANAMA, 19 June 1978, G. B. Small Jr. (X-3886) (USNM).

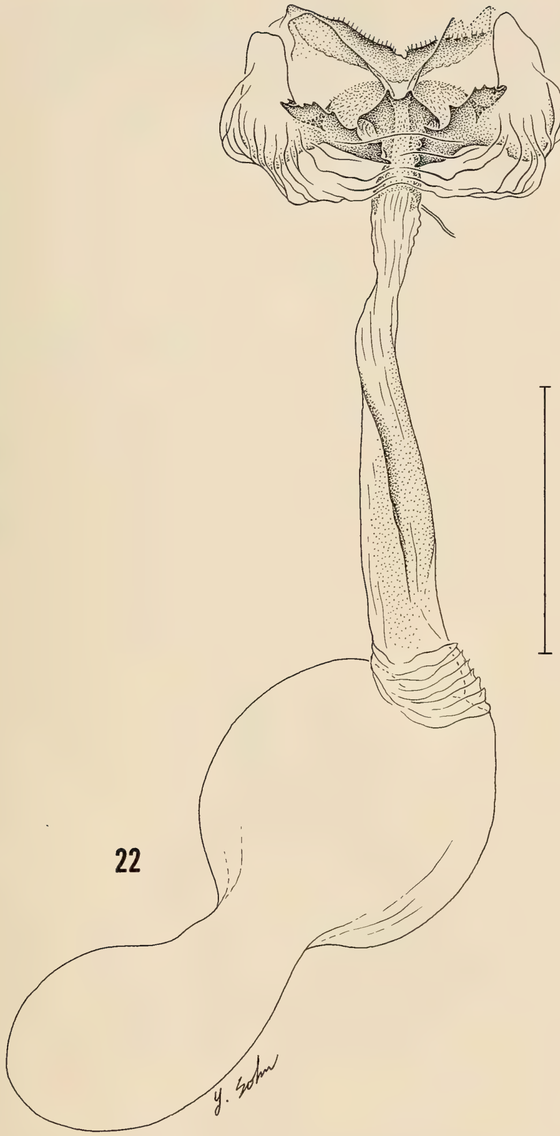

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FIG. 22. Female genitalia of *Cephise guatemalaensis* (allotype of *Polythrix guatemalaensis* Freeman) from X-Can, Quintana Roo, MEXICO, 26 July 1962, E. C. Welling (X-3901) (AMNH). Sterigma, bursa copulatrix, and part of ductus seminalis in ventral view. Scale=2.0 mm. Development of posterior margin of sterigma a bit abnormal, with dorsal layer slightly atrophied, and ventral layer somewhat hypertrophied, on right side. Distalmost extension of hypertrophied right ventral layer, and both ovipositor lobes, not shown because damaged.

TABLE 1. Frequency of antennal nudum variants in species of *Cephise*.

Species	Mean	Number of nudum segments						N
		21	22	23	24	25	26	
C. nuspesez	24.6	—	1	3	15	26	6	51
C. auginulus	23.5	1	7	12	13	6	2	41
C. guatemalaensis	23.5	—	—	1	1	—	—	2
C. nr. *callias*	24.0	—	—	—	2	—	—	2
C. orima	23.5	—	—	1	1	—	—	2
C. hydarnes	23.5	—	—	1	1	—	—	2

to assign names from a heap of seeming synonyms. Evans (1952:154) recognized a single, wide-ranging, tailless (lobed) species with the two subspecies *cephise* and *hydarnes*, which, from his own caricatures (Evans 1952:pl. 23, D.6), are genitalically too divergent to be anything but separate species (a point made by Freeman 1970). Evans gave three synonyms—*zopyrus* Plötz (1881), described from a female from Surinam; *glarus* Mabille (1888), described from a male from the lower Amazon; and *orita* Schaus (1902), described from a female from Peru—for *cephise* Herrich-Schäffer (1869), which was described from a male from no one knows where. And he gave two synonyms—*maneros* Mabille (1888), described from a female from Brazil; and *orima* Schaus (1902), described from a male from Petrópolis, Brazil—for *hydarnes* Mabille (1876), which was described from a female from eastern Brazil. There is no guarantee that these really are synonyms or even that the names *cephise* and *hydarnes* are correctly applied. I know from close examination of Schaus's type, on the one hand, and Evans's text and genitalia figures, on the other, that, contrary to Evans, *orima* is not a synonym of *hydarnes*—at least not of *hydarnes* sensu Evans. Compare the male genitalia of the type of *orima* Schaus (Figs. 3, 4) with those of *hydarnes* in the sense of Evans (1952) and also of Hayward (1948) before him (Figs. 1, 2)—and keep in mind that the lone specimen from which Mabille (1876) described *hydarnes* was female instead of male. The taxonomic stew thickens because *Cephise* is geographically widespread and rare in collections, which makes it harder to detect sibling species and to associate sexes correctly.

Although I lack the material for general treatment of species, my unique handle on *Cephise* is a pair of long, cumulative series of reared specimens from one locality (Guanacaste Conservation Area) in northwestern Costa Rica: 17♂ 11♀ of the tailed *C. auginulus* and 39♂ 30♀ of a new tailless species, *C. nuspesez*. Besides their great utility for assessing sexual dimorphism and individual variation, these series point to a critical evolutionary pattern in *Cephise*: the larvae of both species eat plants in the two families Malpighiaceae and Combretaceae. *Cephise auginu-*

TABLE 2. Larval foodplants of two species of *Cephise* in the Guanacaste Conservation Area of northwestern Costa Rica (Janzen & Burns, unpubl. data). Numbers show males and females reared from each plant species between 1981 and 1995.

	C. nuspesez (tailless)		*C. auginulus* (tailed)	
	♂	♀	♂	♀
COMBRETACEAE				
Combretum farinosum H.B.K.	1	1	7	4
ERYTHROXYLACEAE				
Erythroxylum havanense Jacq.	—	—	—	1
MALPIGHIACEAE				
Banisteriopsis muricata (Cav.) Cuatrec.	1	1	3	3
Heteropteris laurifolia A. Juss.	2	1	1	—
Heteropteris obovata (Small) Cuatrec. & Croat	25	20	1	1
Hiraea reclinata Jacq.	2	2	2	1
Mascagnia polycarpa T. S. Brandegee	8	5	—	—
RUBIACEAE				
Calycophyllum candidissimum (Vahl) DC.	—	—	2	1
	39	30	16	11

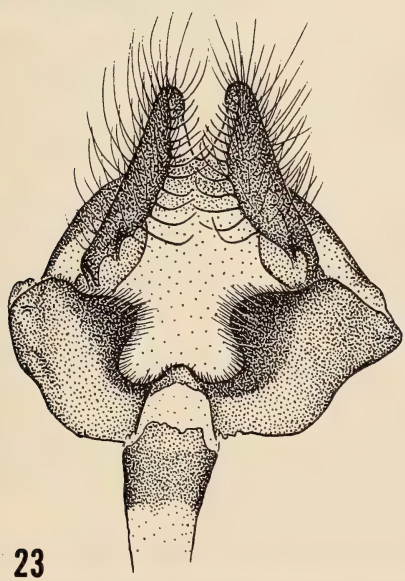

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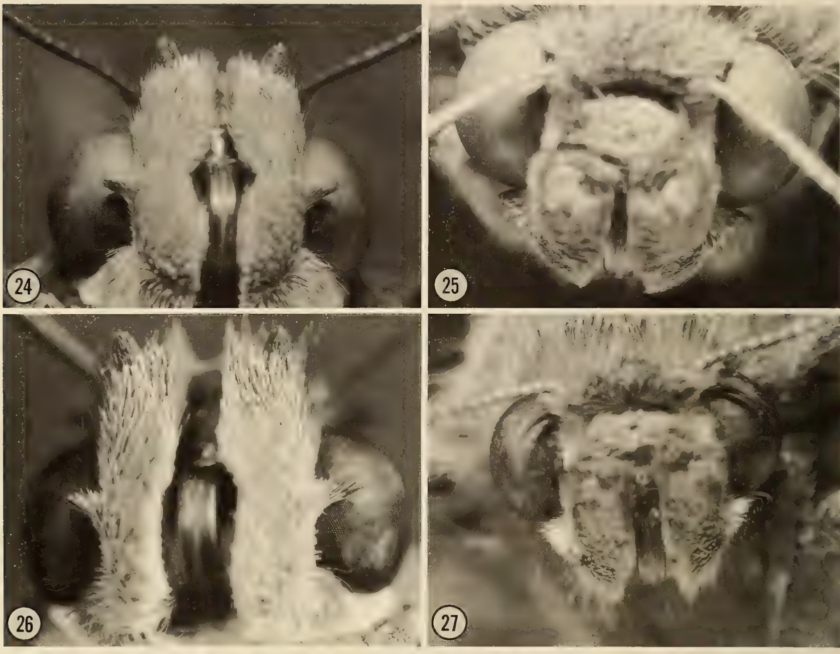
FIG. 23. Beginning of ductus bursae, sterigma, and especially the ovipositor lobes of female *Autochton cellus* (Boisduval & Le Conte), in ventral view, to show major setae directed inward, toward each other, from inner, ventral edges of those lobes, as usual for *Urbanus* group females. Specimen from Hda. Montecristo, Cerro Miramundo, 2300 m, Metapán, EL SALVADOR, 21 May 1972, S. & L. Steinhauser (J. M. Burns 1378) (AME).



FIGS. 24–27. Distinctive prominent scaling (beneath eyes) at distal ends of first palpal segments in reared males of *Cephise* from the Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (USNM), in ventral (left) and anterior (right) views. **24, 25,** *Cephise nuspesez* (a tailless species), rearing voucher 94-SRNP-7535. **26, 27,** *Cephise auginulus* (a tailed species), rearing voucher 93-SRNP-5721.

lus is more catholic because it also eats plants in two other families (Erythroxylaceae and Rubiaceae) for a total of seven known species of foodplants; but, significantly, it eats five of the six plants that *Cephise nuspesez* eats (Table 2).

At this point I have fulfilled my primary purpose of expanding the genus *Cephise* conceptually and redefining it. However, in the course of conveying a modified generic gestalt, I have illustrated not only the reared tailless and tailed species that I have in series but also various odd specimens at hand—especially all three relevant Schaus types (USNM), and their genitalia, in order to promote correct application of specific names in the future. For now, I can do no more with species than describe the new one and offer various comparative comments.

The male of the new species from Costa Rica superficially looks like the type of *Cephise orima* from Petrópolis, Brazil, and is genitalically so close to it that in 1982, when I had only one Costa Rican specimen, I could not exclude the possibility that their slight genitalic differences

stemmed from individual variation. Much later, in a series of Costa Rican males, the differences held, indicating separate species.

Cephise nuspesez, new species
(Figs. 5–7, 18, 19, 28–31)

Male genitalia (Figs. 5–7). Differences between *nuspesez* and most other figured species of *Cephise* (Figs. 1, 2, 8–16) extensive and obvious, but differences between *nuspesez* and *orima* (Figs. 3, 4) limited (chiefly to valva) and relatively subtle: in lateral view, valva of *nuspesez* (Fig. 6) neither as high proximally nor as attenuate (and twisted) distally as that of *orima* (Fig. 4), and dorsodistal corner of proximal section of valva, in *nuspesez*, with short, backward projection (long and slender in *hydarnes* [Fig. 2]) not present in *orima*.

Female genitalia (Figs. 18, 19). Most like those of *orita* (Fig. 17); but, in *nuspesez*, medial edges of paired, heavily sclerotized, ventromedially directed, sterigmal plates flanking **Y** more nearly parallel to midventral line in ventral view, and sclerotized roof of flared part of **Y** more restricted, extending less far caudad.

Facies (Figs. 28–31). As in other tailless (lobed) species of *Cephise*, strong sexual dimorphism in forewing hyaline spots: pale yellow in male, white in female. (In tailed species such dimorphism ranges from slightly less pronounced [*guatemalaensis*] to unapparent [*auginulus*].) Band-and-spots pattern of ventral hindwing weak (Figs. 29, 31) as in other tailless species (Figs. 33, 35, 37) plus *auginulus* (Figs. 39, 41, 43), not strong as in the tailed *callias*, nr. *callias* (Figs. 45, 47), and *guatemalaensis* (Figs. 49, 51). Narrow white fringe on outer margin of hindwing checkered (Figs. 28–31) as in other tailless species (Figs. 34–37) and, to lesser degree, *guatemalaensis* (Figs. 50, 51), instead of uncheckered as in remaining tailed species (Figs. 38–43, 46, 47). Pale outer edging (in space 1c) to dark band of ventral hindwing weak (Fig. 29) to nonexistent (Fig. 31), rather than strong as in *orita* (Fig. 37).

Size. Close to that of other species of *Cephise*, with females averaging 1 mm more than males in forewing length: mean forewing length in males 21.3 mm, range 19.6–22.9 mm, n 34; in females, mean 22.3 mm, range 20.8–24.0 mm, n 24. (Measurements perhaps a bit below those of wild-caught adults, on average; but artificial rearing time highly variable, depending on instar of larva when found [which varied from first to last].)

Nudum (Table 1). Mean number of nudum segments 24.6 (range 22–26, n 51); on average, one segment more than in *auginulus*.

Types. *Holotype*: COSTA RICA, GUANACASTE PROVINCE, Guanacaste Conservation Area, Santa Rosa Sector (10°51'N, 85°37'W), D. H. Janzen & W. Hallwachs, rearing voucher 81-SRNP-646, ♂, Genitalia No. X-1345 J. M. Burns 1981; deposited in National Museum of Natural History, Smithsonian Institution (USNM). *Paratypes*: 38♂ 30♀, COSTA RICA, GUANACASTE PROVINCE, Guanacaste Conservation Area, dry forest, rain forest, and transitional, D. H. Janzen & W. Hallwachs, rearing vouchers between 1989 and 1995; deposited in USNM and in Instituto Nacional de Biodiversidad (INBio), Heredia, Costa Rica. 1♀, COSTA RICA, GUANACASTE PROVINCE, Comelco, 8 km N Bagaces, 50 m, 18 January 1974, P. A. Opler; in collection of C. D. MacNeill.

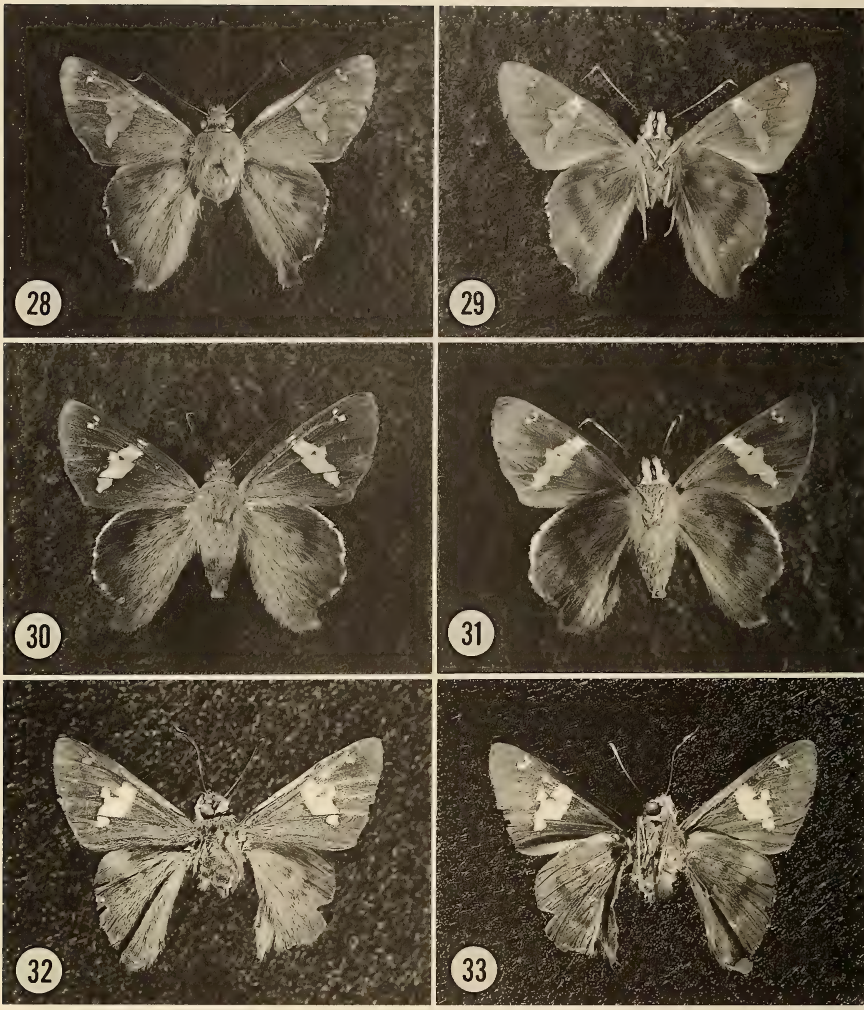
I have seen 2♂ 1♀ *Cephise* from 6 mi (ca. 10 km) S Ciudad Valles, SAN LUIS POTOSI, MEXICO, June 1969, H. A. Freeman, in the American Museum of Natural History, New York, which I suspect may be *nuspesez*; but not having seen their genitalia, I cannot be sure.

Etymology. The name of this new species is a noun in apposition which phonetically says that this species is new. The combination *Cephise nuspesez* is deliberately euphonius.

Peculiarities of some species of *Cephise*

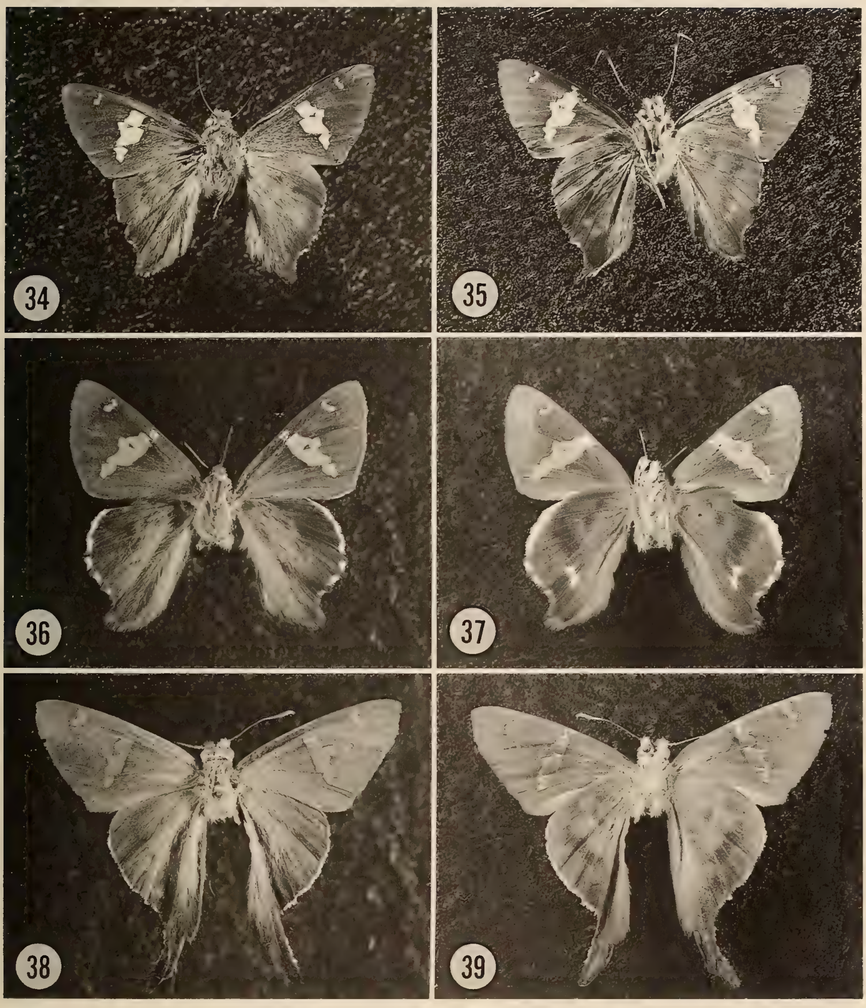
Judging from Evans (1952:pl. 23, fig. D.6.*cephise*), the valva of *Cephise cephise* is about like that of *orima* and *nuspesez* except for a long, slender, backward projection, from the dorsodistal corner of its proximal section, as in *hydarnes* (Fig. 2; Evans 1952:pl. 23, fig. D.6.*hydarnes*).

I refer to one of the tailed species of *Cephise* as "near *callias*" for the



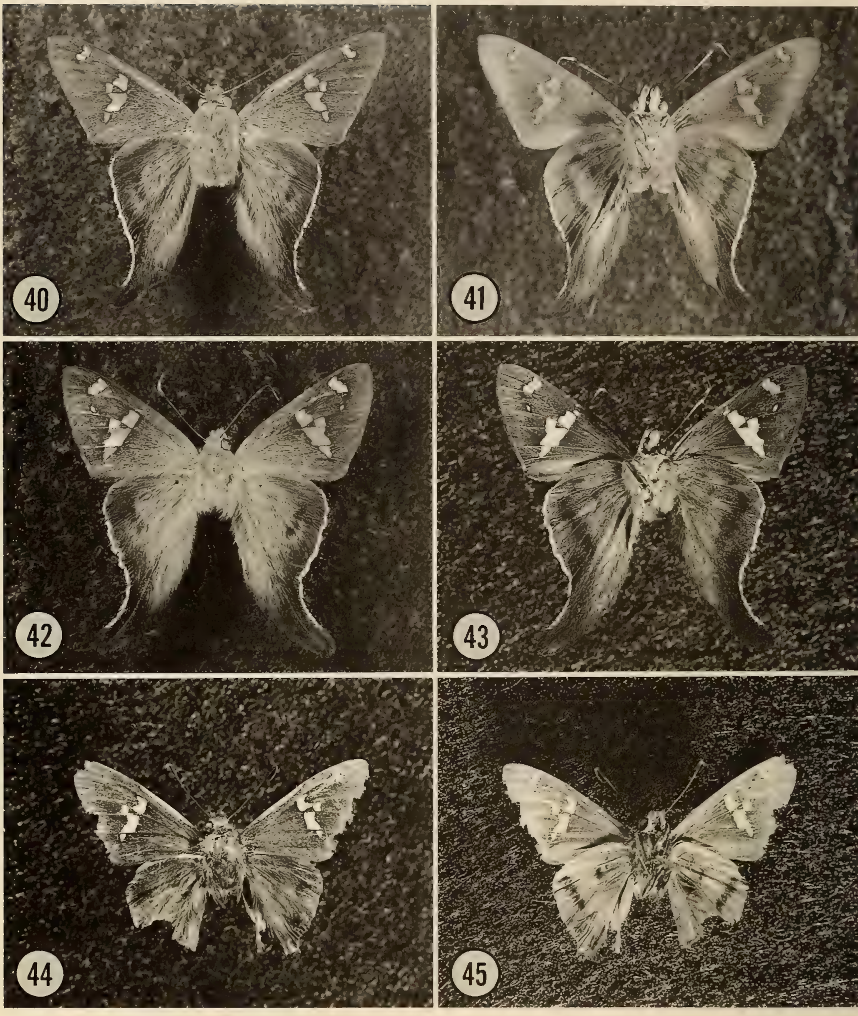
FIGS. 28–33. Adults of *Cephise* in dorsal (left) and ventral (right) views (all ×1, USNM). **28, 29,** *C. nuspesez* ♂, holotype, Santa Rosa Sector, Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 81-SRNP-646, dissection X-1345). **30, 31,** *C. nuspesez* ♀, paratype, Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 94-SRNP-7524). **32, 33,** *C. hydarnes* ♂, PARAGUAY (X-1400).

following reasons. Both the brief original description of *callias*, with a black and white figure (Mabille 1888), and a fuller, subsequent description, with a much better color figure (Mabille & Vuillot 1891), mention and show a bold distal spot in space 7 of the ventral hindwing as well as a bold proximal spot in the same space. The bold distal spot is missing



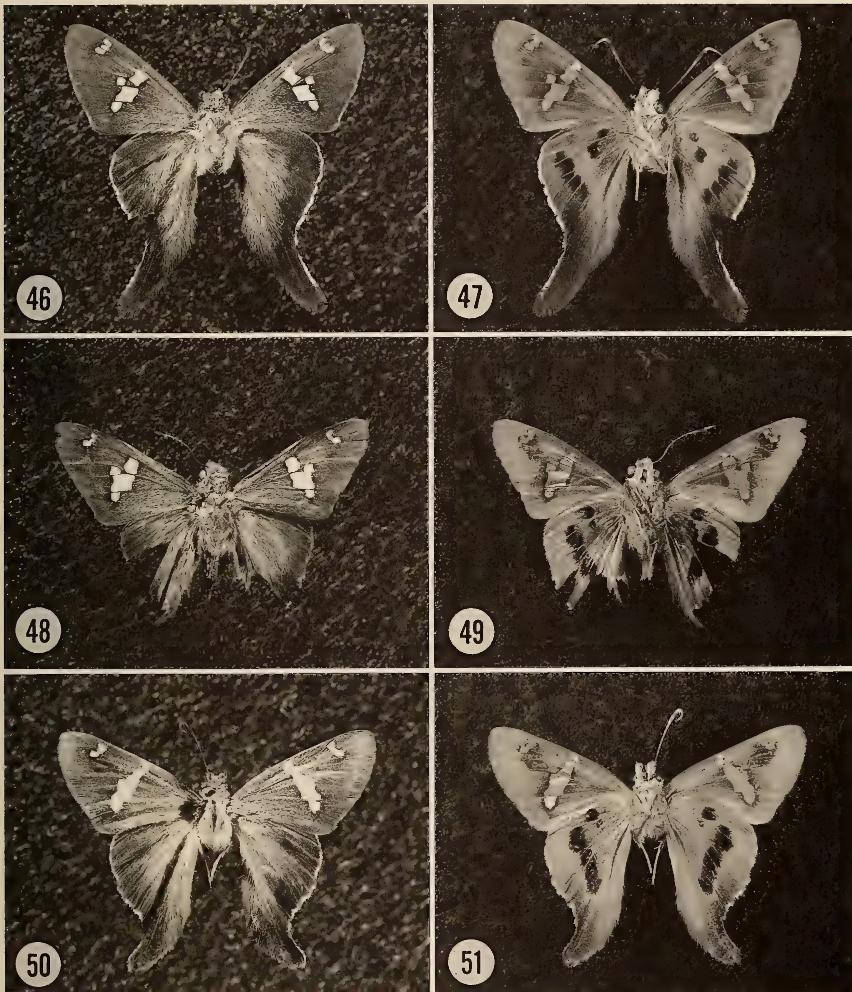
FIGS. 34–39. Holotypes of species of *Cephise* described by Schaus in dorsal (left) and ventral (right) views (all ×1, USNM). **34, 35,** *C. orima* ♂, Petrópolis, BRAZIL (X-1401). **36, 37,** *C. orita* ♀, supposedly from PERU but probably from BOLIVIA (X-3885). **38, 39,** *C. callicina* (=*auginulus*) ♀, HONDURAS (X-3884).

not only from my lone male (Fig. 45) whose genitalia (Figs. 11–13) approximate Evans's (1952:pl. 15, fig. C.7.6) caricature of *callias* genitalia but also from the lone female (Fig. 47) that I tentatively associate with this male. These specimens come, respectively, from French Guiana and Panama, to either side of Porto Cabello, Venezuela, the source of the lone female from which *callias* was described (Mabille & Vuillot 1891).



FIGS. 40–45. Adults of *Cephise* in dorsal (left) and ventral (right) views (all ×1, USNM). **40, 41,** *C. auginulus* ♂, Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 93-SRNP-3800, dissection X-3801). **42, 43,** *C. auginulus* ♀, Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 93-SRNP-3647, dissection X-3881). **44, 45,** *C.* nr. *callias* ♂, Saül, 200–450 m, 3°37' N, 53°43' W, FRENCH GUIANA, 16 November 1993, D. J. Harvey (X-3900).

Although the spot difference may involve individual variation, the male and female in question may represent a *callias* sibling. Evans's lone specimen from which he figured the male genitalia of what he considered *callias*, came from Bolivia (Evans 1952). Since it is already clear



FIGS. 46–51. Adults of *Cephise* in dorsal (left) and ventral (right) views (all ×1). **46, 47,** *C.* nr. *callias* ♀, Paraíso, Canal Zone, PANAMA, 19 June 1978, G. B. Small Jr. (X-3886) (USNM). **48, 49,** *C. guatemalaensis* ♂, holotype, Sayaxché, Petén, GUATEMALA, 23 August 1963, E. C. Welling (Freeman genitalic dissection no. H-674) (AMNH). **50, 51,** *C. guatemalaensis* ♀, allotype, X-Can, Quintana Roo, MEXICO, 26 July 1962, E. C. Welling (X-3901) (AMNH).

that genitalia can be closely similar in separate species of *Cephise*, far more specimens are needed.

The dorsal extension of the anteroventral, innermost edge of the valva is hypertrophied and dentate (in different ways) in the tailed species *auginulus* (Fig. 9; Godman & Salvin 1893, pl. 75, fig. 22) and nr. *callias*

(Fig. 12). (This may also be true of *guatemalaensis* [Fig. 15], but damage in the genitalic dissection of the only known male precludes judgment.) The juxta is visibly enlarged anteriorly in the tailed species *auginulus* (Fig. 9), nr. *callias* (Fig. 12), and perhaps *guatemalaensis* (Fig. 15)—though here again, damage in the critical region makes it hard to interpret. However, the juxta is hugely enlarged anteriorly in the tailless *hydarnes* (Fig. 2).

The distal end of the valva is the most strikingly variable feature across all figured species (Figs. 2, 4, 6, 9, 12, 15). The dentate, distal ends of the valvae are conspicuously asymmetric in *hydarnes*, with the right valva longer than the left. The distal end of the uncus is extra wide in *hydarnes* (Fig. 1) and in *guatemalaensis* (Fig. 14). The anterior end of the aedeagus is exceptionally long and narrow, and usually is curved downward and bent slightly to the right, in *auginulus* (Figs. 9, 10).

The ductus bursae exhibits three major variations: one in the tailless *orita* (Fig. 17) and *nuspesez* (Figs. 18, 19), a second in the tailed *auginulus* (Fig. 20) and nr. *callias* (Fig. 21), and a third—the most outré—in the tailed *guatemalaensis* (Fig. 22). The paired, heavily sclerotized, sterigmal plates flanking the **Y** are more elaborate in the tailless *orita* (Fig. 17) and *nuspesez* (Figs. 18, 19), and especially in the tailed *guatemalaensis* (Fig. 22), than they are in the tailed *auginulus* (Fig. 20) and nr. *callias*, which is the simplest of all (Fig. 21). On the other hand, nr. *callias* has a unique, large, midventral, caudally projecting plate developed from the floor of the **Y** (Fig. 21). A small, narrow, rounded, midventral ridge, which distinctly notches the posterior margin of the lamella postvaginalis midventrally, is unique to *auginulus* (Fig. 20).

Judging from the female (Figs. 50, 51) because they are completely broken off of the male (Figs. 48, 49), the hindwing tails of *guatemalaensis* are significantly shorter than those of the other tailed species (Figs. 38–47). The female of *guatemalaensis* (Figs. 50, 51) is the only specimen of *Cephise* I have seen (out of 135 examined) that lacks a small, dark, more or less triangular bit of ground color between the small hyaline spot in space 3 and the large hyaline spots in space 2 and the cell of the forewing (Figs. 28–49). Since this is the sole known female of *guatemalaensis*, I cannot say whether such variation in the hyaline band is individual or meaningful.

The morphology of *Cephise* indicates a genus that is highly distinct but also internally complex with a long evolutionary history.

THE *CYDA* GROUP OF *CODATRACTUS*

Although the species *cyda* Godman has been in *Codatractus* from the beginning, when Lindsey (1921) proposed this name to replace *Heteropia* Mabille (a junior homonym), the other two species now joining

cyda to form a distinctive, compact group of tailless *Codatractus* have never been near this genus. Both *Codatractus mysie* (Dyar), **new combination**, and *Codatractus uvydixa* (Dyar), **new combination**, were originally described in *Thorybes* early in this century (Dyar 1904, 1914); and since then they have had a nomenclatural history more checkered than the fringes of their wings (Figs. 79–84).

This is particularly true of *mysie* which, because it was described from the "Patagonia Mountains, Arizona," became part of the U.S. fauna and had to be treated repeatedly, whether it was known or not. It was placed in *Eudamus (Phaedinus)* [sic] by Skinner (1911), in *Phoedinus* by Lindsey (1921) and Lindsey et al. (1931), in *Cogia (Phoedinus)* by Skinner & Williams (1922), in *Caicella* (a Hemming replacement name) by Bell (1938), Hoffmann (1941), and Tilden (1949), and was argued back to *Phoedinus* by Tilden (1975), where he left it (Tilden & Smith 1986). Meanwhile, Evans (1952) listed both *mysie* and *uvydixa* (which was described from the "Sierra de Guerrero, Mexico") as synonyms of *Thorybes valeriana* (Plötz), though he added that *uvydixa* was "Possibly a sub-species." Thereafter, Miller (1970), MacNeill (1975), Miller and Brown (1981), and Scott (1986) all dealt with *mysie* as *Thorybes valeriana*. On the other hand, Llorente-Bousquets, Luis-Martínez, and Vargas-Fernández (1990) listed *mysie* and *uvydixa* as species of *Thorybes* separate from *Thorybes valeriana*. Ferris (1989), following both Tilden's (1949) argument for the validity of *mysie* as a species and Evans's (1953) placement of *Phoedinus* as a junior synonym of *Cogia*, put *mysie* in *Cogia*. As a result, *mysie* still goes by totally different names in contemporary butterfly books: *Cogia mysie* according to Bailowitz and Brock (1991:43) who, however, "strongly feel that *mysie* is sufficiently distinct in phenotype and behavior to warrant placement in its own genus"; and *Thorybes valeriana* according to Brown et al. (1992).

The name *valeriana* cannot apply to *mysie* or *uvydixa*. At the British Museum of Natural History I closely studied Plötz's unpublished color painting of his *Eudamus valeriana*, and have directly compared an excellent color photograph of it with many specimens of *Codatractus*, including *mysie* and *uvydixa*. Besides serious discrepancies in color pattern, each antenna of the painted skipper has a club with a long and only moderately swollen body that abruptly dwindles to a very short, delicate, and sharply reflexed apiculus. All species of *Codatractus*, including all three species of the *cyda* group, have an unusual antennal club: it is basally stout and apically tapered but evenly arcuate throughout its length—nothing is sharply reflexed, and it is impossible to distinguish an apiculus (Figs. 79–90).

Characterization of the *cyda* group. In the *cyda* group, as opposed to the rest of *Codatractus*, the distal segment of the palpus is ex-

TABLE 3. Forewing length (mm) in males of the *cyda* group of *Codatractus*.

Species	N	Range	Mean	SE	SD	CV
C. mysie	37	18.7–23.7	21.05	0.19	1.13	5.37
C. cyda	12	22.5–25.4	24.33	0.23	0.78	3.21
C. uvydixa	31	24.5–27.9	26.49	0.15	0.82	3.11

ceptionally long. (As in all species of *Codatractus*, males lack a costal fold.)

In the male genitalia of *Codatractus* the valva is distally divided into dorsal and ventral parts; the ventral part extends dorsad just posterior to the dorsal part and becomes dentate distally (Figs. 52–58). In lateral view the dorsal extension is more smoothly curved and broader in the *cyda* group (Figs. 52–56)—especially in *cyda* (Fig. 56) and *uvydixa* (Figs. 54, 55)—than in any other species of *Codatractus* (Figs. 57, 58). (To represent the "other species of *Codatractus*" in visual comparisons with the *cyda* group, I have selected *C. imalena* [Butler], a tailless species and the type of the genus, and *C. carlos* Evans, a tailed species. But my written characterizations come from close comparisons of all the species in the genus.) In profile the tegumen is more humped in the *cyda* group (Figs. 52–56) than in any other species of *Codatractus* (Figs. 57, 58). In dorsal view the distal end of the uncus is narrow and essentially undivided in the *cyda* group (Figs. 59–63) but wide and deeply bilobed in three species (Fig. 64) to very wide and deeply divided into prongs in all other species of *Codatractus* (Fig. 65). The elaborate cornutus within the aedeagus suggests a fan with many sharp fingers in the *cyda* group (Figs. 52–56, 66–70), but has either a narrow, central shaft to which the longer, spike-like fingers attach (Figs. 57, 71) or little more than a base for their attachment, usually in two clusters (Figs. 58, 72), in other species of *Codatractus*.

In figuring and describing the male genitalia of *mysie*, Tilden (1949) erroneously wrote that "the aedeagus has but a single internal spicule"; and in figuring them (as *valeriana*), Miller (1970:fig. 3) erroneously showed nothing more than a single, simple spike inside the aedeagus. Neither saw the sharply fingered fan described here which is diagnostic of the *cyda* group.

In the female genitalia of *Codatractus* a large plate originates ventrad of the ostium bursae and extends posteriad to about the posterior edge of the lamella postvaginalis. Midventrally, in all species of *Codatractus* outside the *cyda* group, this elongate plate is shallowly to (usually) deeply (Fig. 77) or very deeply (Fig. 78) notched, leaving a pair of prongs still united anteriorly so as to hide the ostium bursae in ventral view (Figs. 77, 78). But in the *cyda* group the plate is divided all the way

TABLE 4. Frequency of antennal nudum variants in species of the *cyda* group of *Codatractus*.

Species	Mean	Number of nudum segments										N
		16	20	21	22	23	24	25	26	27	28	
C. mysie	22.3	1	2	6	12	18	5	—	—	—	—	44
C. cyda	25.4	—	—	—	—	—	—	7	3	1	—	11
C. uvydixa	26.4	—	—	—	—	—	—	5	9	13	2	29

to its anterior end, splitting it into left and right halves and exposing the ostium bursae in ventral view (Figs. 73–76).

Distinguishing the species of the *cyda* group. Genitalia. Although *Codatractus mysie*, *C. uvydixa*, and *C. cyda* form a morphologically tight group, they do have their differences. The dorsal extension of the ventral division of the distal end of the valva is not as broad in lateral view in *mysie* (Figs. 52, 53) as it is in *uvydixa* (Figs. 54, 55) and *cyda* (Fig. 56). Put another way, in *uvydixa* the dorsal and ventral divisions of the valva are about equally broad (Figs. 54, 55), and in *cyda* the ventral division may even be slightly broader than the dorsal division (Fig. 56); but in *mysie* the ventral division is distinctly narrower than the dorsal division (Figs. 52, 53). The distal dentation of the dorsal extension of the ventral division is less in *mysie* (Figs. 52, 53) than it is in *uvydixa* (Figs. 54, 55) and *cyda* (Fig. 56). Most of the ventral surface of the paired lobes of the lamella postvaginalis is densely clothed with short setae in *uvydixa* (Figs. 74, 75) and *cyda* (Fig. 76), while dense setal clothing is limited to the posterior part of these lobes in *mysie* (Fig. 73). (Females of the *cyda* group are rare in collections; with additional material, this difference may not hold up.)

Size. The three species of the *cyda* group differ strikingly in size, with *uvydixa* the largest and *mysie* the smallest. (Indeed, *mysie* is the smallest species of *Codatractus*.) Males of *cyda* are over 3 mm more than males of *mysie* in average forewing length but still about 2 mm less than males of *uvydixa* (Table 3).

Antenna. Although *uvydixa* averages about 1 nudum segment more than *cyda* and 4 nudum segments more than *mysie*, what is so remarkable is that there is no overlap between *mysie* and the other two species in number of nudum segments (Table 4). I have never encountered such nudum variation among related species.

Facies. Both pairs of wings—especially the hindwings—are perceptibly narrower in *cyda* (Figs. 85, 86) than in *uvydixa* and *mysie* (Figs. 79–84). This is related to the fact that *cyda* has a small but unmistakable lobe at the end of hindwing vein 1b (Figs. 85, 86) that is reduced though still detectable in *uvydixa* (Figs. 81–84) and mostly to entirely (Figs. 79,

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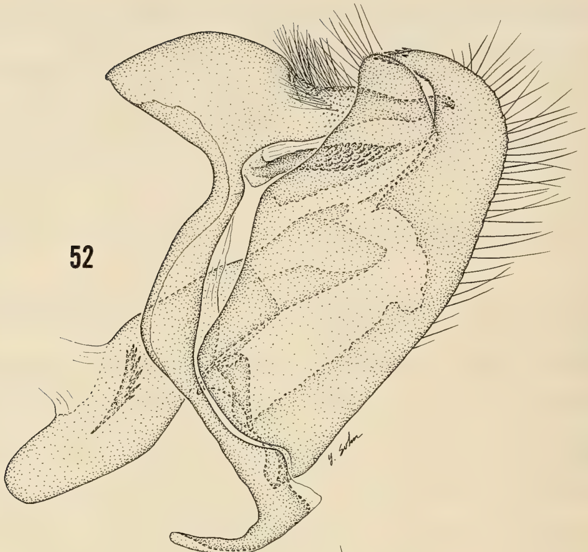

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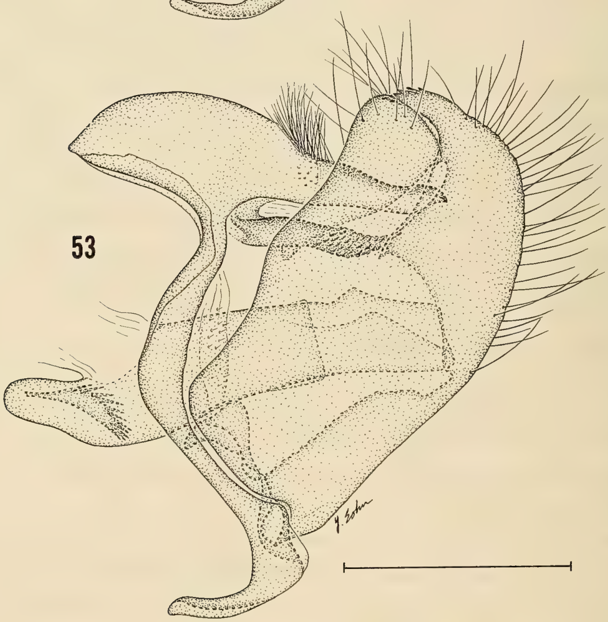

FIGS. 52, 53. Male genitalia (minus right valva) of *Codatractus mysie* (in the *cyda* group of *Codatractus*) in left lateral view (USNM). Scale=1.0 mm. **52,** Lectotype, Patagonia Mountains, Arizona, USA, 21 May 1903 (genitalic dissection no. W[illiam] D. F[ield] 2950). **53,** Cuesta Colorada, Hidalgo, MEXICO, 3 March 1981, W. H. Howe (J. M. Burns genitalic dissection no. X-1936).

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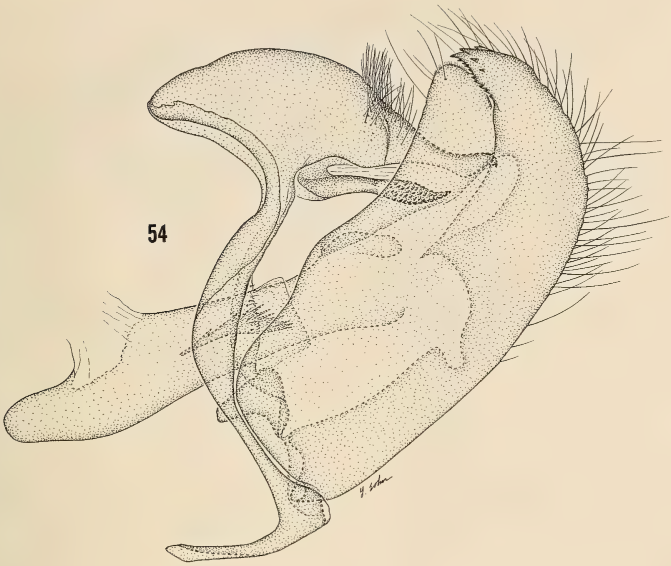

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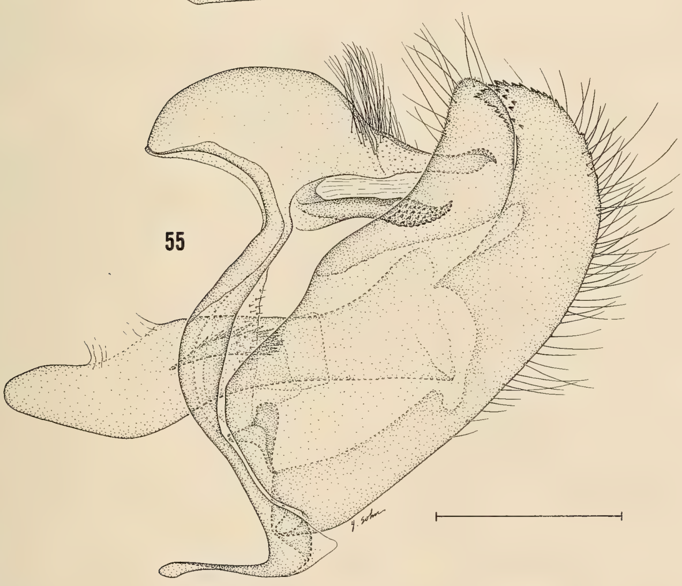

FIGS. 54, 55. Male genitalia (minus right valva) of *Codatractus uvydixa* (in the *cyda* group of *Codatractus*) in left lateral view (USNM). Scale=1.0 mm. **54,** Dark differentiate, Mazatlán, Sinaloa, MEXICO (X-1941). **55,** Holotype, Sierra de Guerrero, MEXICO, June 1913, R. Müller (X-1940).

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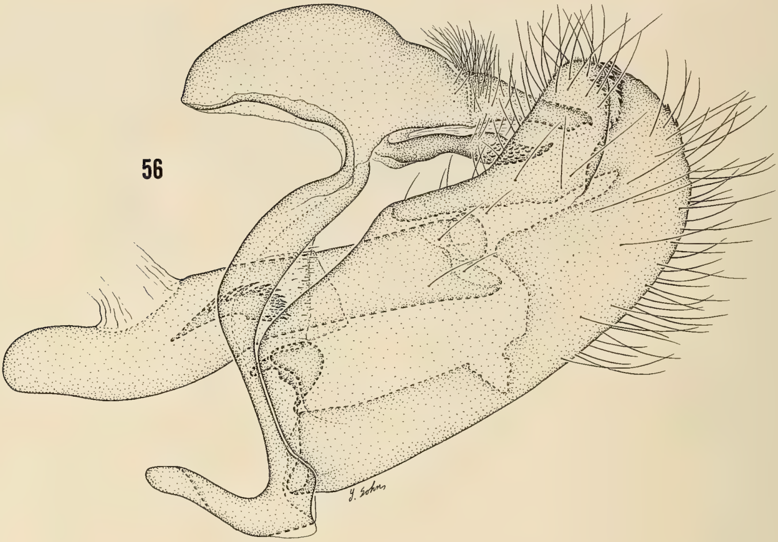

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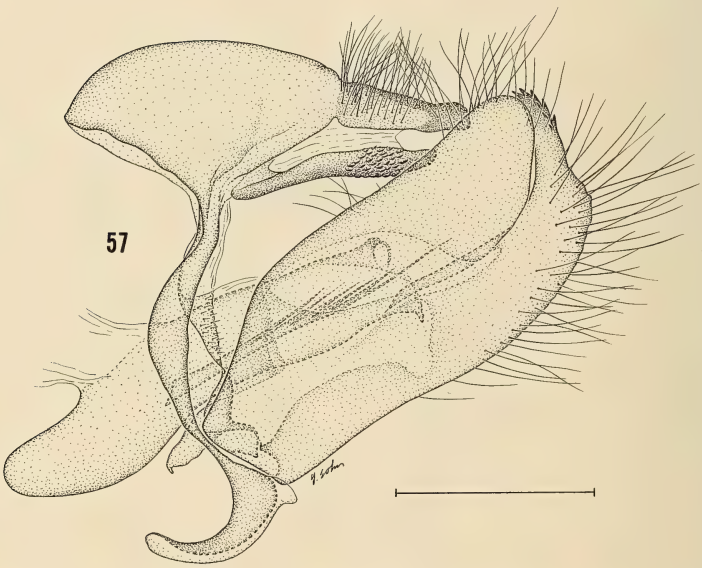


FIGS. 56, 57. Male genitalia (minus right valva) of two species of *Codatractus* in left lateral view. Scale=1.0 mm. **56,** *C. cyda*, automatically in the *cyda* group of *Codatractus*, San Pedro Sula, HONDURAS, 1895, E. Wittkugel (J. M. Burns 1439) (BMNH). **57,** *C. imalena*, the type species of *Codatractus*, Avangarez, COSTA RICA, July (X-1371) (USNM).

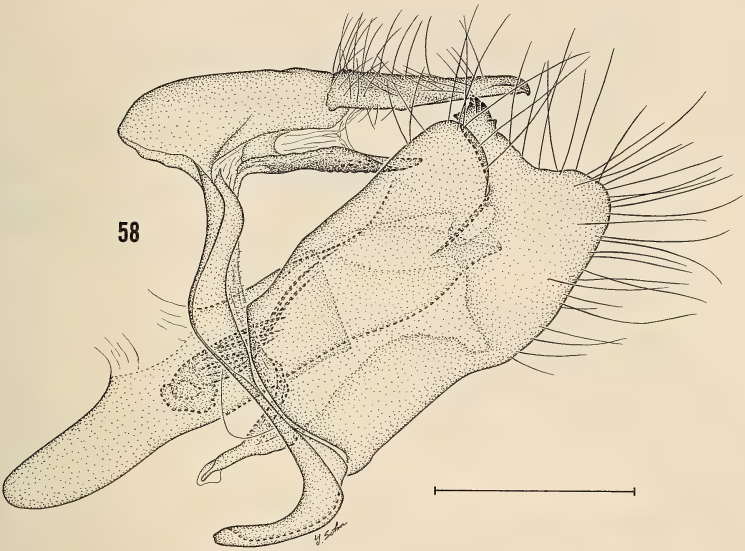
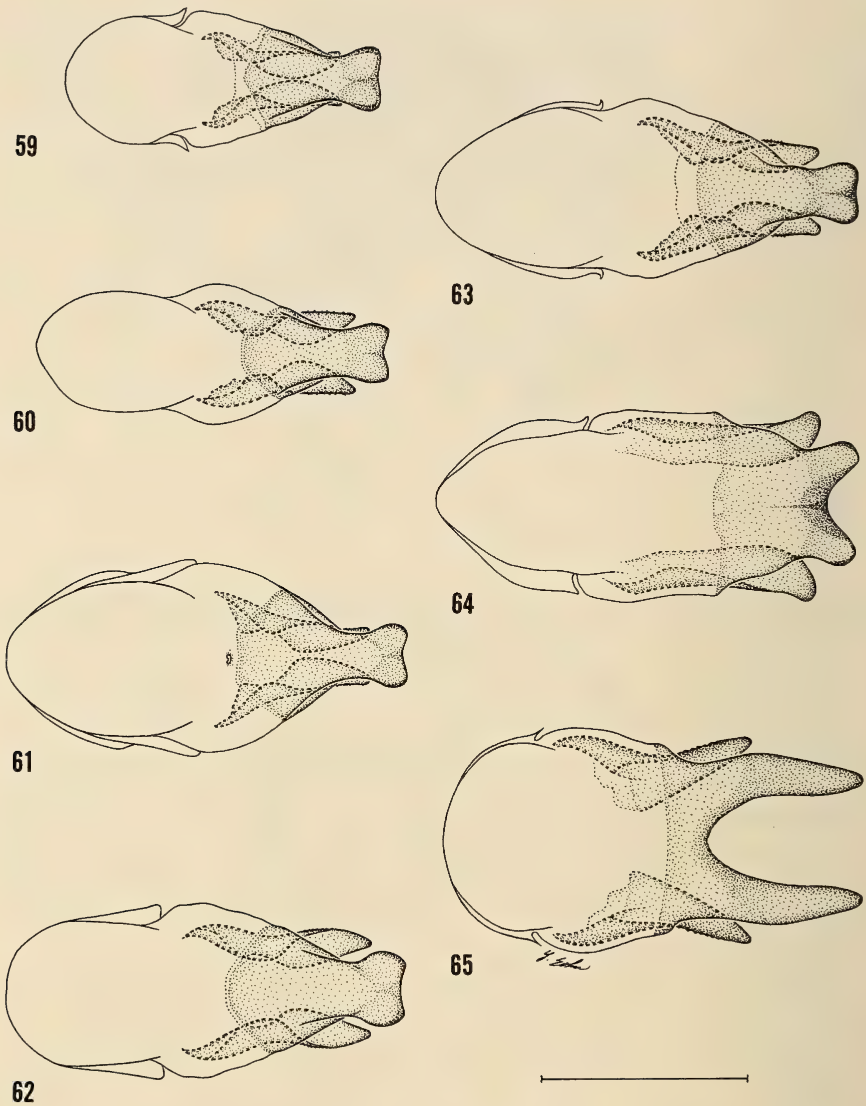


FIG. 58. Male genitalia (minus right valva) of *Codatractus carlos*, a tailed species, in left lateral view. Scale=1.0 mm. Córdoba, Veracruz, MEXICO, June 1909, R. Müller (J. M. Burns 1420) (USNM).

80) eliminated in *mysie* (*mysie* has the roundest wings of any species of *Codatractus*—compare Figs. 79–90). The hyaline spots of the forewing are expressed more fully by *cyda* (Figs. 85, 86) than by *uvydixa* (Figs. 81–84) and *mysie* (Figs. 79, 80). (As usual in skippers, such spots are expressed more fully by females than by males.) In general, the strong checkering of the wing fringes is slightly more discrete in *cyda* and *mysie* than it is in *uvydixa*.

On the ventral hindwing, *cyda* always exhibits a strong white patch adjacent to the lower outer margin (Fig. 86). A similar patch, more variably—and less strongly—expressed, appears in those populations of *uvydixa* (in Chiapas, Puebla, and Guerrero—Fig. 84) that are geographically closer to *cyda*, but not in those populations of *uvydixa* that are farther away (in Colima, Jalisco, and Sinaloa—Fig. 82). The latter, which I simply call the "*uvydixa* dark differentiate," look more like *mysie* (Fig. 80), except, of course, for their giant size. Dorsally, golden hairlike scales—on the basal half of the forewing (proximal to the hyaline spots), and over most of the hindwing below the costal margin—which contrast with the dark brown ground color in typical *uvydixa* (Fig. 83), are replaced by essentially concolorous hairs in the *uvydixa* dark differentiate (Fig. 81).



FIGS. 59–65. Tegumen, uncus, and gnathos of the male genitalia of five species of *Codatractus* (including all three species of the *cyda* group) in dorsal view. Scale=1.0 mm. **59,** *C. mysie*, lectotype, Arizona, USA (W[illiam] D. F[ield] 2950). **60,** *C. mysie*, Hidalgo, MEXICO (X-1936). **61,** *C. uvydixa*, dark differentiate, Sinaloa, MEXICO (X-1941). **62,** *C. uvydixa*, holotype, Sierra de Guerrero, MEXICO (X-1940). **63,** *C. cyda*, San Pedro Sula, HONDURAS (J. M. Burns 1439). **64,** *C. imalena*, the type species of *Codatractus*, Avangarez, COSTA RICA, July (X-1371). **65,** *C. carlos*, a tailed species, Veracruz, MEXICO (J. M. Burns 1420).

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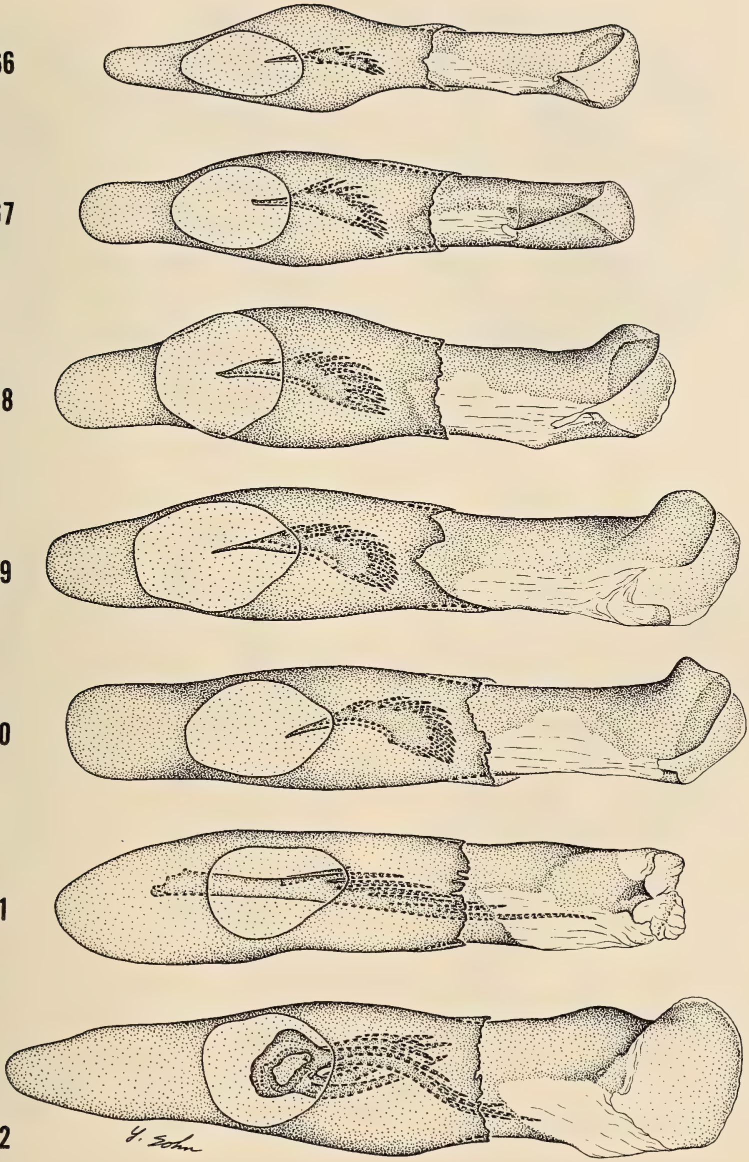
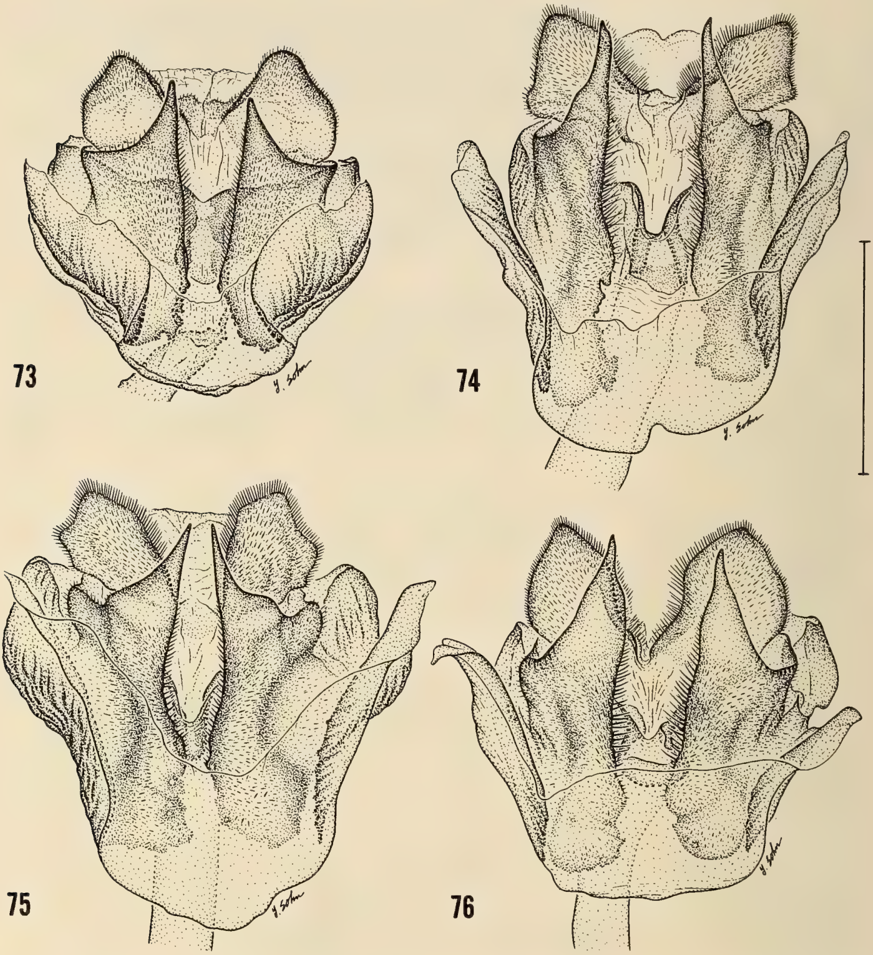
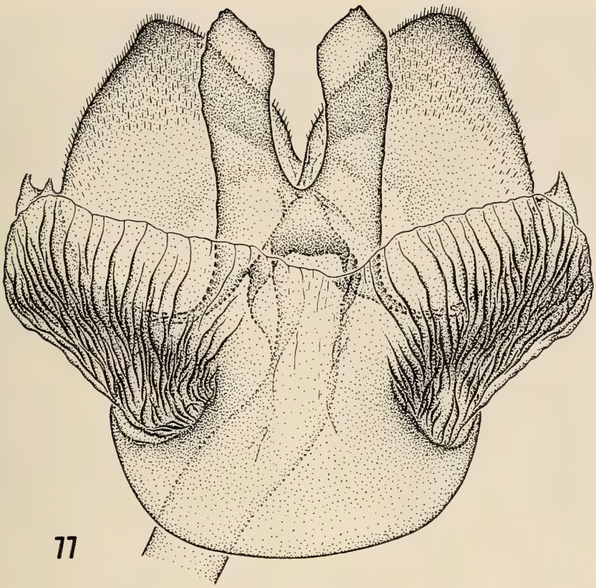


FIGS. 66–72. Aedeagus of the male genitalia of five species of *Codatractus* (including all three species of the *cyda* group) in dorsal view. All drawn to the same scale. **66,** *C. mysie*, lectotype, Arizona, USA (W[illiam] D. F[ield] 2950). **67,** *C. mysie*, Hidalgo, MEXICO (X-1936). **68,** *C. uvydixa*, dark differentiate, Sinaloa, MEXICO (X-1941). **69,** *C. uvydixa*, holotype, Sierra de Guerrero, MEXICO (X-1940). **70,** *C. cyda*, San Pedro Sula, HONDURAS (J. M. Burns 1439). **71,** *C. imalena*, the type species of *Codatractus*, Avangarez, COSTA RICA, July (X-1371). **72,** *C. carlos*, a tailed species, Veracruz, MEXICO (J. M. Burns 1420).



FIGS. 73–76. Sterigma and beginning of ductus bursae of the female genitalia of all three species of the *cyda* group of *Codatractus* in ventral view. Scale=1.0 mm. **73,** *C. mysie*, Guadaloupe, MEXICO, R. Müller (X-1944) (USNM). **74,** *C. uvydixa*, Acahuizotla, Guerrero, MEXICO, July 1957, T. Escalante (X-2080) (AME). **75,** *C. uvydixa*, Las Delicias, 700 m, 60 km SW Comitán, Chiapas, MEXICO, June 1969, P. Hubbell (X-2081) (AMNH). **76,** *C. cyda*, Las Delicias, 700 m, 60 km SW Comitán, Chiapas, MEXICO, June 1969, P. Hubbell (X-2083) (AMNH).

Larval foodplants. *Codatractus mysie* oviposits on, and feeds as a larva on, *Tephrosia leiocarpa* Gray (Leguminosae) in southern Arizona (Roever 1990). This bolsters an emerging pattern. Other species of *Codatractus*, as far as known, also choose legumes: in southern Arizona the tailless *C. arizonensis* (Skinner) was seen to oviposit on *Eysenhardtia or-*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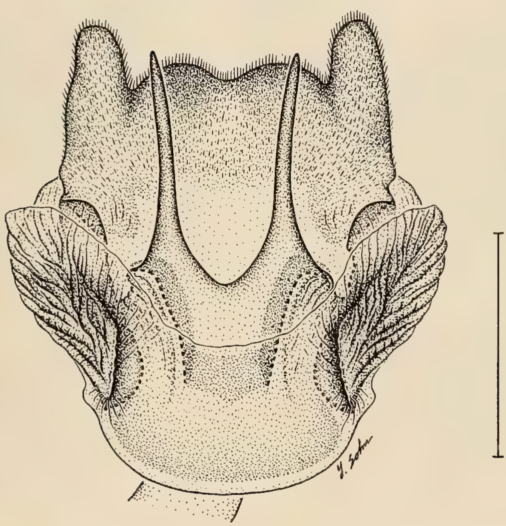
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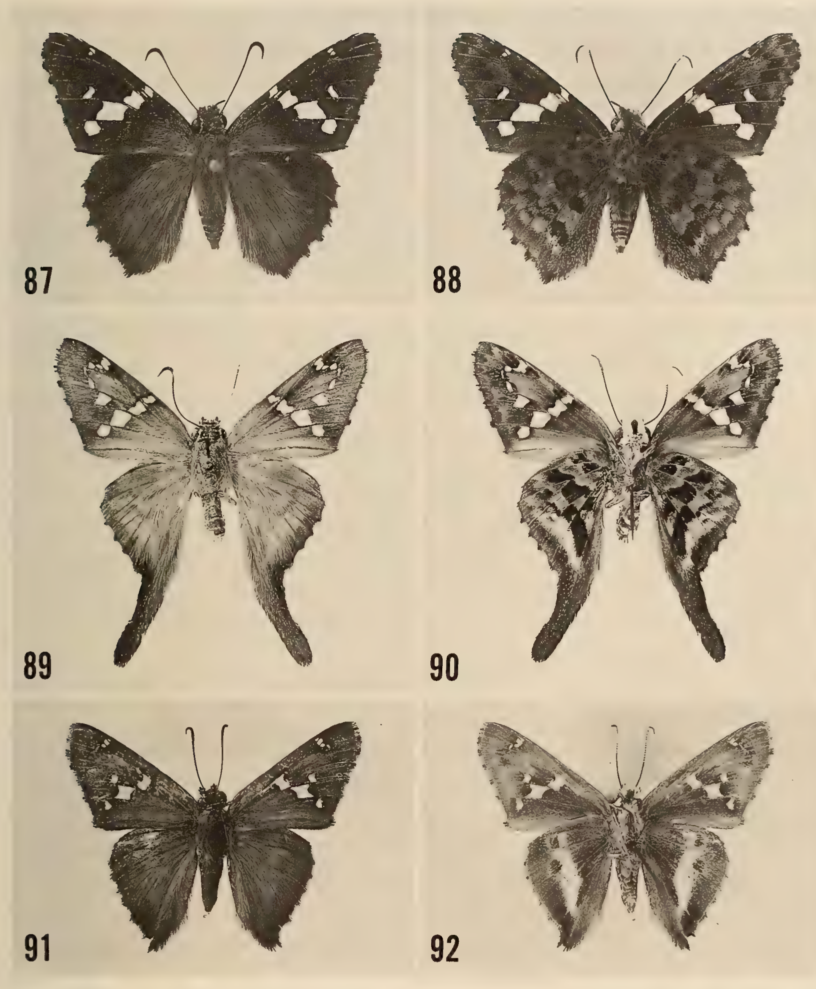
FIGS. 77, 78. Sterigma and beginning of ductus bursae of the female genitalia of two species of *Codatractus* in ventral view. Scale=1.0 mm. **77,** *C. imalena*, the type species of *Codatractus*, Cerro Campana, 2500 ft [760 m], PANAMA, 26 November 1964 (G. B. Small) (J. M. Burns 1433) (USNM). **78,** *C. carlos*, a tailed species, Cayuga, GUATEMALA, November (X-2025) (USNM).

FIGS. 79–86. Males of the *cyda* group of *Codatractus* in dorsal (left) and ventral (right) views (all ×0.95). **79, 80,** *C. mysie*, lectotype, Patagonia Mountains, Arizona, USA, 21 May 1903 (W[illiam] D. F[ield] 2950) (USNM). **81, 82,** *C. uvydixa* dark differentiate, Mazatlán, Sinaloa, MEXICO (X-1942) (USNM). **83, 84,** *C. uvydixa*, holotype, Sierra de Guerrero, MEXICO, June 1913, R. Müller (X-1940) (USNM). **85, 86,** *C. cyda*, San Pedro Sula, HONDURAS, 1895, E. Wittkugel (BMNH).



FIGS. 87–92. Males of a tailless species of *Codatractus*, a tailed species of *Codatractus*, and a tailless species erroneously placed in *Codatractus* in dorsal (left) and ventral (right) views (all ×0.95). **87, 88,** *C. imalena*, the type species of *Codatractus*, Cerro Hornito, 1200 m, Chiriquí, PANAMA, 27 July 1975, G. B. Small (USNM). **89, 90,** *C. carlos rowena* Evans, holotype, Patao, Güiria, VENEZUELA, August 1891 (BMNH). **91, 92,** Holotype of what Dyar called *Eudamus hyster*, Sierra de Guerrero, MEXICO, July 1913, R. Müller (J. M. Burns 1424) (USNM).

thocarpa (Gray) Wats. and larvae were found on it (Roever 1990 [gave plant as *E. polystachya* (Ortega) Sarg.], Bailowitz & Brock 1991); the tailless *C. melon* (Godman & Salvin) was reared from larvae on *Lonchocarpus acuminatus* (Schlechtendal) M. Sousa S., *L. orotinus* Pittier,

and especially *L. minimiflorus* Donn. Smith in northwestern Costa Rica (Janzen & Burns, unpubl. data); and larvae of the tailed *C. alcaeus* (Hewitson) were eating *Ichthyomethia communis* Blake and *Amerimnon granadillo* Standley in northeastern Mexico (Kendall & McGuire 1975) and *Lonchocarpus minimiflorus* in northwestern Costa Rica (Janzen & Burns, unpubl. data).

Geographic distribution of the *cyda* group. The three species of this group closely replace one another geographically (Fig. 93). Their virtual parapatry reinforces the already compelling morphologic basis for uniting them. I fret about the state of New World skipper systematics when the bringing together of species from three different genera yields such a tidy example of allopatric speciation.

Codatractus mysie ranges from southeastern Arizona, mostly in mountains of western and central Mexico, to Oaxaca—but also occurs in Baja California Sur; *C. uvydixa* ranges in a strip down the western side of Mexico from Sinaloa to Chiapas; and *C. cyda* occurs in a relatively limited area from eastern Chiapas to northwestern Honduras (Fig. 93). Although *cyda* and *uvydixa* in eastern Chiapas provide the only apparent instance of contact, others may surface with more material. I would not be surprised, for instance, to find *uvydixa* and *mysie* sympatric in southern Puebla and Oaxaca.

Adding *mysie* and *uvydixa* to *Codatractus* does not increase the grand geographic distribution of this genus.

Material examined. I have examined the type specimens (all male) of the species in the *cyda* group: the holotype of *Heteropia cyda* Godman, the holotype of *Thorybes uvydixa* Dyar (Figs. 55, 62, 69, 83, 84), and what I am designating below as the lectotype of *Thorybes mysie* Dyar (Figs. 52, 59, 66, 79, 80). Dyar (1904:40) wrote that *mysie* was "described from two specimens, Patagonia Mountains, Arizona (E. J. Oslar). *Type.*—No. 7737, U. S. National Museum." Two specimens in the USNM come from the Patagonia Mts, Ariz, 5/21/03, and bear a red type label with that type number. The genitalia are gone from one but dissected and preserved from the other ("♂ genitalia, 1948, W.D.F. 2950") which I proclaim the **lectotype.**

Codatractus mysie. USA: ARIZONA: SANTA CRUZ COUNTY: Atascosa Mountains, Peña Blanca Lake, 4000 ft [1220 m], 31°24' N, 111°5' W, 5-VIII-1991, 2♀, J. M. & S. N. Burns (USNM). Pajarito Mountains, Alamo Canyon, 4000–4200 ft [1220–1280 m], K. Roever (Roever): 2-VIII-1974, 2♂; 27-VII-1978, 4♂ 1♀; 24-VII-1983, 1♂. Patagonia, 3 mi [5 km] SW, 2-VIII-1976, 1♂ 1♀, R. A. Bailowitz (USNM). Rt. 82, 3–4 mi [5–6 km] SW Patagonia, 3900–4100 ft [1190–1250 km], K. Roever (Roever): 24-VII-1977, 1♂; 18-VII-1986, 2♂; 24-VII-1986, 1♂ 1♀. Patagonia Mountains, 21-V-1903, 1♂ [LECTOTYPE] 1?, Oslar (USNM). Patagonia Mountains, 3 mi [5 km] SSW Harshaw, 5400 ft [1645 m], 31°26' N, 110°43' W, 8-VIII-1991, 1♀, J. M. & S. N. Burns (USNM).

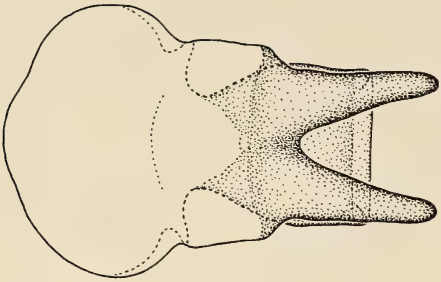
MEXICO: BAJA CALIFORNIA SUR: Ayo. Candelaria, 26-XI-1961, 1♂ (MacNeill). Bahia de la Concepcion, 10-IX-1968, 2♂, C. Callaghan (AME). CHIHUAHUA: Hidalgo

FIG. 93. Geographic distribution (based on specimens examined) of the *cyda* group of *Codatractus*, which strongly reflects allopatric speciation. Large open circles, *C. cyda*; open triangles, *C. uvydixa*; solid triangles, *C. uvydixa* dark differentiate; and small solid circles, *C. mysie*. Open symbols mark differentiates with considerable white on the ventral hindwing (see Figs. 83–86). The one known instance of sympatry involves *C. cyda* and *C. uvydixa* in eastern Chiapas, Mexico.

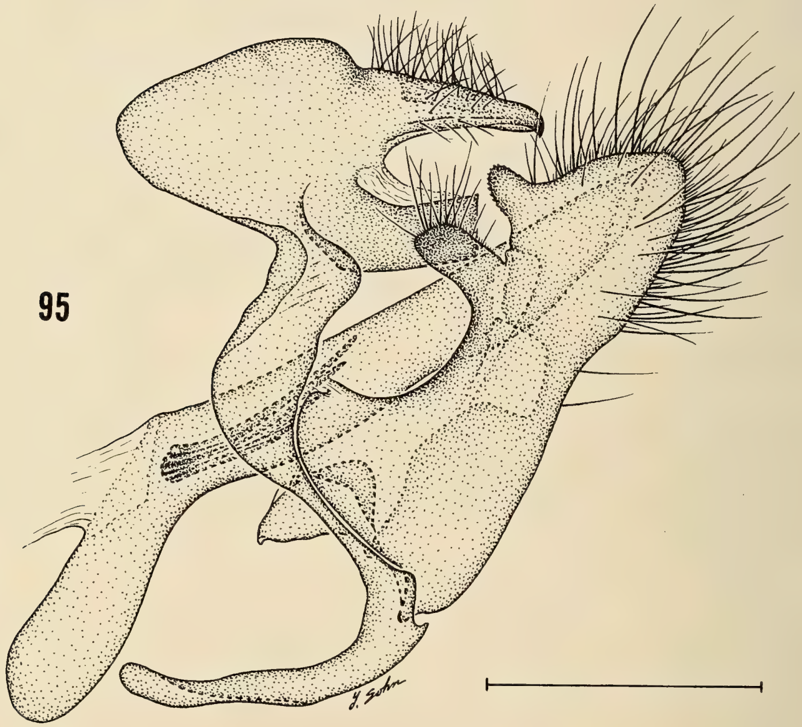
del Parral, 25 mi [40 km] W, 6800 ft [2075 m], 15-VII-1964, 1♂, J. Powell (MacNeill). Matachic, 7-VII-1947, 1♂, C. D. Michener (AMNH). DISTRITO FEDERAL: Los Reyes, 7500 ft [2285 m], 2-VII-1952, 4♂ 2♀, E. E. Gilbert, C. D. MacNeill (UCB, MacNeill). Sierra de Guadalupe, VII-1917, 1♂, C. C. Hoffmann (AMNH). HIDALGO: Cuesta Colorada, W. H. Howe: 15-III-1980, 2♂ (AMNH); 3-III-1981, 1♂ (USNM). OAXACA: Hwy. 175, 5 mi [8 km] N Oaxaca, 6000 ft [1830 m], J. Kemner (USNM): 22-VII-1988, 1♂; 26-VII-1991, 2♂. Hwy. 175, 5–10 mi [8–16 km] N Oaxaca, 6000–7000 ft [1830–2135 m], 3-VIII-1992, 1♂, J. Kemner (USNM). QUERETARO: Ahuacatlan, 19 km SSW, 1500 m, 21°16' N, 99°8' W, 16-III-1984, 1♂, J. Rawlins, D. Harvey, S. Thompson (CMNH). SONORA: Guaymas, Oslar (BMNH): 24-II-1903, 2♂; 25-II-1903, 1♀. ZACATECAS: Fresnillo, J. Stone (AMNH): 24-VI-1950, 1♂; 25-VI-1950, 1♂. STATE UNDETERMINED: Guadaloupe, 1♂ 1♀, R. Müller (USNM).

***Codatractus uvydixa* dark differentiate.** MEXICO: COLIMA: La Salada, 1000 ft [305 m], R. Wind (AME): 21-V-1968, 1♂; 30-V-1968, 1♂. Salada, R. Wind (AMNH): 10-V-1967, 1♂; 11-V-1967, 1♂; 20-V-1967, 2♂ + 1♂ in private collection; 4-VI-1967, 1♂; 10-VI-1967, 1♂; 8-V-1968, 1♂. JALISCO: Zenzontla, SE El Grullo, 800 m, 8-VI-1994, 1♂, A. D. Warren. SINALOA: Mazatlan, 2♂ (USNM).

***Codatractus uvydixa*.** MEXICO: CHIAPAS: El Aguacero, 2-V-1988, 5♂, J. Kemner



94



95

FIGS. 94, 95. Male genitalia of holotype of *Eudamus hyster* Dyar, Sierra de Guerrero, MEXICO, July 1913, R. Müller (J. M. Burns 1424) (USNM). The species *hyster* was transferred to *Codatractus* where obviously it does not belong (compare true *Codatractus* male genitalia in Figs. 52–72). Scale=1.0 mm. **94,** Tegumen, uncus, and gnathos in dorsal view. **95,** Complete genitalia (minus right valva) in left lateral view.

(USNM); Las Delicias, 60 km SW Comitan, 700 m, VI-1969, 1♀, P. Hubbell (AMNH); Rizo de Oro, 25-IV-1972, 1♂, H. L. King (AME). GUERRERO: Acahuizotla, T. Escalante (AME): VII-1957, 2♂ 1♀; VII-1959, 1♂; XI-1960, 5♂. Balsas, 1♂ (AMNH). Mexcala, VIII-1958, 1♂, T. Escalante (AME). Sierra de Guerrero, VI-1913, 1♂ [HOLOTYPE], R. Müller (USNM). PUEBLA: Jaulillas, 18-V-1979, 1♂, J. R. Powers (USNM).

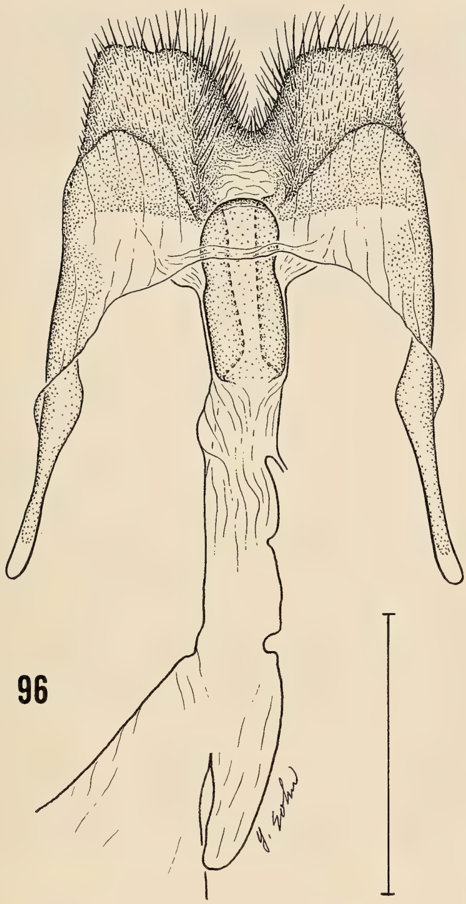


FIG. 96. Sterigma and ductus bursae of the female genitalia of ? *hyster* in ventral view (*hyster* obviously does not belong in *Codatractus*: compare true *Codatractus* female genitalia in Figs. 73–78). Scale=1.0 mm. 12 mi [19.3 km] W Ocozocoautla, 2500 ft [760 m], Chiapas, MEXICO, 26 July 1952, E. E. Gilbert, C. D. MacNeill (X-2042) (MacNeill).

Codatractus cyda. HONDURAS: San Pedro Sula, 1895, 10♂, E. Wittkugel (BMNH) [HOLOTYPE lacks year and first name of collector]. MEXICO: CHIAPAS: Las Delicias, 60 km SW Comitan, 700 m, VI-1969, 2♂ 1♀, P. Hubbell (AMNH).

The *hyster*ectomy of *Codatractus*

One species put in *Codatractus* by Evans (1952:80) does not belong: what was described—again from the "Sierra de Guerrero, Mexico," by Dyar (1916)—as *Eudamus hyster*. Evans (1952:42) had reservations about his own pigeonholing; for, after remarking that "*hyster* has usually been placed next *asander* in the genus *Aguna*, but structurally it is very

different," he went on to say that "it has been moved to *Codatractus*, where it is better placed, though not a perfect fit."

Clearly the genitalia of *hyster* in the male (Figs. 94, 95) as well as the female (Fig. 96) do not conform with those of male (Figs. 52–72) and female (Figs. 73–78) *Codatractus*. Besides the total differences in *hyster*'s female genitalia and the salient differences in the shape and relative proportions of its male valva, note that the gnathos of *hyster* is continuous across its distal end (Fig. 94) instead of divided into left and right sclerotized parts (Figs. 59–65) as it is in all species of *Codatractus*; that the saccus is long (Fig. 95) instead of short (Figs. 52–58) as it is in all species of *Codatractus*; and that the aedeagus is relatively much longer (Fig. 95) than it is (Figs. 52–58) in any species of *Codatractus*. Moreover, the pattern of *hyster*'s ventral hindwing (Fig. 92) does not really fit the *Codatractus* mold (Figs. 80, 82, 84, 86, 88, 90).

Some behavior of *hyster* is also aberrant. Warren (1995, pers. comm.), who observed *hyster* together with several species of *Codatractus* along small creeks in Jalisco, Mexico, says that *hyster* perched mainly on small branches just above or next to the water but *Codatractus*, mainly on mud; that *hyster* was less easily disturbed, less fast and direct in its flight, and less deliberate about alighting than *Codatractus*; and that *hyster* did not attract perched *Codatractus*, which did, however, fly up at other *Codatractus*. Kendall (1976) reported that larvae of *hyster*, in Tamaulipas, Mexico, were gregarious, rather than solitary like other skipper larvae (which include the known larvae of *Codatractus*).

Although I am still unsure where it goes, I am formally removing *hyster* from *Codatractus*. Better unattached than misplaced. This is the first *hyster*ectomy I have ever performed, and *Codatractus* is instantly healthier for it.

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ESTIMATES OF GENETIC DIFFERENTIATION AMONG *CALLOSAMIA* SPECIES AND *HYALOPHORA CECROPIA* (SATURNIIDAE) USING ALLOZYME ELECTROPHORESIS

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ABSTRACT. The saturniid silk moths *Callosamia promethea*, *C. angulifera*, and *C. securifera* can be hybridized by hand-pairing but are apparently reproductively isolated in the wild by temporal differences in mating times. Cross-attraction of pheromones among species and the occasional disruption of normal flight and calling rhythms by local weather conditions may result in incomplete reproductive isolation by allochronic mating behavior. Intergeneric hybrids of *Callosamia* and *Hyalophora* also can be produced through hand-pairing. We performed cellulose acetate electrophoresis of the three *Callosamia* species, *C. angulifera* X *C. promethea* hybrids, and *Hyalophora cecropia* to estimate the amount of genetic differentiation among taxa. Each of the three *Callosamia* species were distinguishable by fixed alleles, an indication that little or no gene flow occurs between the species. Nei's genetic identities between species pairs (calculated across 18 loci) ranged from 0.76 to 0.79, suggesting equal differentiation among the three taxa. The electrophoretic profile of *Hyalophora cecropia* was substantially different; our samples shared alleles with *Callosamia* at only 1 of the 18 loci.

Additional key words: Attacini, reproductive isolation, *Callosamia promethea*, *Callosamia angulifera*, *Callosamia securifera*.

The attacine saturniid silk moths are represented in North America by five genera: *Callosamia*, *Hyalophora*, *Rothschildia*, *Samia*, and *Eupackardia*. Although Michener (1952) considered *Callosamia* a subgenus of *Hyalophora*, Ferguson (1972) felt the three species represented a discrete group and elevated *Callosamia* to generic rank. The three *Callosamia* species share a number of morphological and ecological similarities, but differ in host use. The promethea moth, *C. promethea* (Drury), is polyphagous on deciduous trees and has a wide geographic range from southern Canada to Florida. The tulip tree silk moth, *C. angulifera* (Walker), is primarily a specialist on tulip tree (*Liriodendron tulipifera* L., Magnoliaceae) and co-occurs with southern populations of *C. promethea* where this host is abundant. The monophagous sweetbay silk moth, *C. securifera* (Maassen), is restricted to the southeastern coastal plain where its host, sweetbay magnolia (*Magnolia virginiana* L., Magnoliaceae) grows. Although all three species utilize magnoliaceous hosts, only *C. securifera* is able to survive on sweetbay

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foliage, which has potent antifeedant and toxic properties towards unadapted insect herbivores (Nitao et al. 1991, 1992).

The three species can be hybridized by hand-pairing but are apparently reproductively isolated in the wild by temporal differences in mating times. In fact, *C. securifera*, which was first described as a variety of *C. angulifera*, only recently was elevated to species status after the temporal isolating mechanism between *Callosamia* species was described (Brown 1972). *Callosamia securifera* females emit pheromone from mid-morning to early afternoon, while *C. promethea* are active from late afternoon to dusk, and *C. angulifera* females do not begin calling until after dusk. There appears to be little or no qualitative difference in the pheromone, as *C. securifera* and *C. angulifera* males can be attracted to calling captive *C. promethea* females (Haskins & Haskins 1958, Peigler 1980, K. S. Johnson unpubl. data).

Hybrids between *Callosamia* species can be obtained by hand-pairing, but hybridization in the wild is believed to be uncommon, since intermediate specimens are rarely collected (Brown 1972, Ferguson 1972, Peigler 1980). Differences in the size of genitalia can prevent successful mating even when moths are hand-paired, as the genitalia of *C. promethea* are considerably larger than those of the other two species (Peigler 1977). Post-mating incompatabilities contribute to reduced egg hatch, weak larvae, disruption of pupal diapause, and weak or malformed adults (Peigler 1980). Interspecific hybrids involving *C. promethea* are usually sterile, although a small proportion of *C. angulifera* X *C. securifera* hybrids are fertile for three generations (Haskins & Haskins 1958, Peigler 1977, 1980). In addition, differences in host plant use may contribute to post-zygotic selection against hybrid larvae. Neither *C. angulifera* nor *C. promethea* can survive on sweetbay magnolia, despite the fact that the former is a near-specialist on another magnoliaceous host, tulip tree, and the latter is highly polyphagous. Understanding the phylogenetic relationships of the *Callosamia* group would provide a valuable framework for testing hypotheses concerning the evolution of host use and physiological adaptation to host chemistry in this group.

Despite the absence of intermediate specimens in the wild, the cross-attraction of the mating pheromone and observations of occasional disruption of normal flight and calling times by local weather conditions raise the possibility that gene flow between the three species may occur. Allozyme electrophoresis has proven to be useful for estimating genetic divergence and phylogenetic relationships of insect taxa at various taxonomic levels (Pashley 1983, Berlocher 1984). We conducted an electrophoretic survey of *C. promethea*, *C. angulifera*, *C. securifera*, *C. promethea* X *C. angulifera* hybrids and *Hyalophora cecropia* allozymes to: 1) evaluate the effectiveness of reproductive isolating mechanisms in

TABLE 1. Collection locations for *Callosamia* specimens used for allozyme electrophoresis; *C. angulifera* from Cass County, Michigan were taken over a two year period.

Taxon	Region	Site	Number of Individuals
C. promethea	Wisconsin	1 Kenosha County	2
	Michigan	2 Otsego County	2
		3 Barry County	4
		4 Clinton County	2
	Maryland	6 Montgomery County	2
C. angulifera	Michigan	5 Cass County	9
	Virginia	7 Greensville County	3
C. securifera	North Carolina	8 Bladen County	1
	Florida	9 Highlands County, site 1	6
		10 Highlands county, site 2	4
		11 Lake County	1

Callosamia; 2) estimate the relative degree of genetic differentiation among the three species; and 3) compare the genetic distances of *Callosamia* to the closely related *Hyalophora cecropia*.

MATERIALS AND METHODS

Representatives of the three *Callosamia* species, *C. promethea* X *C. angulifera* hybrids, and *Hyalophora cecropia* (selected for outgroup comparison) were included in this study. Individuals of *Callosamia* were field-collected or were offspring of females collected from two to seven sites within their natural geographic ranges. The number of individuals per site ranged from 1 to 6, and because females were needed for other studies during this period, most of the samples for electrophoresis were males. Hybrid *C. promethea* X *C. angulifera* came from a semi-natural mating of a captive female *C. promethea* (collected in southern Wisconsin) with a wild *C. angulifera* male (Cass County, Michigan). This female released pheromone at dusk and attracted 7 wild *C. angulifera* males; viable hybrids (n=6) were obtained from one mating. An additional hybrid specimen was the result of a male *C. promethea* hand-paired with a female *C. angulifera*. *Hyalophora cecropia* pupae were collected from several sites in Ingham and Clinton counties, Michigan in 1991. Voucher specimens have been deposited at the museum of the Entomology Department at Michigan State University.

Both adults and pupae were used in allozyme analyses after preliminary studies indicated that there were no appreciable differences in allozyme frequencies between the life stages. Individuals were killed by freezing at -80°C and stored until processing. The posterior half of the abdomen of adult moths and pupae was used for electrophoresis. Tissue was homogenized in 250 ul of extraction buffer (Tris-EDTA-B-mercap-

TABLE 2. Allozymic loci resolved for *Callosamia promethea*, *C. angulifera*, *C. securifera* and *Hyalophora cecropia*, and corresponding running conditions for each enzyme. Buffers and origin positions (an=anode, ce=center, ca=cathode) were selected to keep enzymes centered on the cellulose acetate plates. Asterisks indicate voltage adjusted to maintain current between 9-12 mA per plate.

Locus	Enzyme name (E.C. number)	Running conditions buffer	origin	voltage	time
AAT-1	Aspartate aminotransferase (2.6.1.1)	I	an	275	40
AAT-2					
AC	Acontinase (4.2.1.3)	A	an	*	40
ACP	Acid phosphatase (3.1.3.2)	C	ce	275	40
ALD	Aldolase (4.1.2.13)	I	ce	275	40
FUM	Fumarase (4.2.1.2)	C	ce	275	40
GPI	Glucose phosphate isomerase (5.3.1.9)	I	—	275	40
G6PDH					
HBDH	Hydroxybutyrate dehydrogenase	D	an	300	40
IDH	Isocitrate dehydrogenase (1.1.1.42)	A	an	*	40
LDH	Lactate dehydrogenase (1.1.1.27)	B	an	*	40
MDH	Malate dehydrogenase (1.1.1.37)	C	ce	275	40
MPI	Mannose-6-phosphate isomerase (5.3.1.8)	I	an	275	40
P3GDH	3-phosphoglycerate dehydrogenase (1.1.1.95)	C	an	275	40
PEP-LA	Peptidase (leucyl-alanyl) (3.4.11–13..)	C	—	275	40
PGM	Phosphoglucomutase (2.7.5.1)	I	an	275	40
SORDH	L-iditol dehydrogenase (1.1.1.14)	I	an	275	40
TPI	Triose phosphate isomerase (5.3.1.1)	I	an	275	40

toethanol, pH 7.0) with a tissue grinder, then centrifuged at 14,000 rpm for 8 minutes. Tissue supernatant (0.25 ul) was applied to cellulose acetate plates using the Super Z-12 application system (Helena Laboratories, Beaumont, Texas). Plates were electrophoresed in refrigerated rigs under the conditions indicated in Table 2, then stained using an agar overlay and covered to prevent back staining. Bands were scored by measuring the relative mobilities of alleles from the origin after arbitrarily assigning the most common allele a mobility value of 100. To insure consistency of scoring between runs, two individuals from each plate were run on the subsequent plate, and at least two species were always represented on a plate.

Genetic divergence between *Callosamia* species was estimated by calculating Nei's pairwise genetic identities (Nei 1978) with jackknifed standard errors across all eighteen loci (Hartl & Clark 1989). Intraspecific patterns of allele frequencies (e.g., Wright's F-statistics, overall heterozygosities) were not calculated due to the small sample sizes.

RESULTS

Eighteen loci were resolved across the taxa surveyed. Six loci showed no variation (ALD, GPI, G6PDH, PEP-LA, SORDH, TPI), but fixed

differences were observed between *Callosamia* species pairs at five loci (AC, ACP, FUM, MDH, and P3GDH), and the remaining seven loci were polymorphic in at least one species. Nine loci were polymorphic in *Hyalophora cecropia* and six were invariant; there was only one shared allele between *Callosamia* and *Hyalophora* (AAT-1). The allele frequencies and relative mobility of allozymes are summarized in Table 3.

Callosamia promethea, *C. angulifera* and *C. securifera* were distinguishable by fixed alleles at three or more loci, as expected for genetically distinct species. There were four fixed differences between *C. securifera* and *C. angulifera* (AC, ACP, FUM, MDH); and three between *C. angulifera* and *C. promethea* (AC, ACP, P3GDH). Genetic identities and jackknifed standard errors calculated from invariant, polymorphic and fixed alleles at all 18 loci indicate that *C. promethea*, *C. angulifera* and *C. securifera* are equally differentiated from each other with genetic identities of 0.76±0.08 (*C. promethea* vs. *C.angulifera*), 0.77±0.08 (*C. promethea* vs. *C. securifera*) and 0.79±0.08 (*C. angulifera* vs. *C. securifera*).

DISCUSSION

Although *Callosamia* species hybridize in captivity, their genomes are quite distinct, as evidenced by the presence of fixed allelic differences among the three taxa. The presence of fixed differences at a single locus is generally accepted as evidence of complete reproductive isolation in sympatric taxa (Menken 1989), and those between *C. promethea* and *C. angulifera* held true even in samples collected from a location where both species were abundant (Cass County, Michigan). These electrophoretic results support the generally accepted view that reproductive isolation between *Callosamia* species in the wild is complete (Ferguson 1972, Peigler 1980). The estimated genetic identities of 0.76, 0.77, and 0.79 between species pairs are within the range of values (0.32 to 0.99) reported in other studies of congeneric Lepidoptera (Stock & Castrovillo 1981, Pashley 1983, Menken 1989, Hagen & Scriber 1991) and are consistent with the view of the genus as a discrete cluster of equally differentiated species.

Although our study revealed no evidence of allelic introgression between *Callosamia* species, we cannot eliminate the possibility that low levels of introgression may occur in some geographic locations. To date, there are few or no quantitative field studies of interspecific attraction and mating frequency in *Callosamia*, and few for other saturniids (Collins & Tusks 1979). Moreover, if hybrid matings do occur, local hybrid zones may exist in parts of the geographical ranges of these moths. Because gene introgression can be assymetrical or severely reduced by post-zygotic incompatibility of hybrids or the mating behavior and ge-

TABLE 3. Allele frequencies for 18 loci resolved in *Callosamia securifera*, *C. angulifera*, *C. promethea*, hybrids and *Hyalophora cecropia*. Sample sizes (number of individuals) listed in parentheses.

AAT-1		(12)	(12)	(11)	(3)	(1)	(5)
	20	0.17	0.00	0.00	0.00	0.00	0.00
	70	0.12	0.04	0.00	0.00	0.00	0.00
	100	0.71	0.46	1.00	1.00	0.00	1.00
	140	0.00	0.50	0.00	0.00	0.00	0.00
	200	0.00	0.00	0.00	0.00	1.00	0.00
AAT-2		(12)	(12)	(12)	(3)	(1)	(5)
	67	0.08	0.08	0.00	0.33	0.00	0.00
	75	0.00	0.00	0.00	0.00	0.00	0.40
	100	0.92	0.92	1.00	0.67	1.00	0.00
	125	0.00	0.00	0.00	0.00	0.00	0.60
HBDH		(12)	(12)	(12)	(7)	(1)	(8)
	–250	0.00	0.00	0.00	0.00	0.00	0.13
	–200	0.00	0.00	0.00	0.00	0.00	0.75
	–100	0.00	0.00	0.00	0.00	0.00	0.13
	50	0.17	0.00	0.04	0.14	0.00	0.00
	100	0.83	1.00	0.96	0.86	1.00	0.00
IDH		(8)	(8)	(7)	(0)	(0)	(0)
	100	0.69	0.69	0.93	—	—	—
	130	0.31	0.31	0.07	—	—	—
LDH		(12)	(12)	(12)	(7)	(1)	(8)
	67	0.00	0.00	0.58	0.00	0.00	0.00
	100	1.00	1.00	0.42	1.00	1.00	0.00
	120	0.00	0.00	0.00	0.00	0.00	0.69
	150	0.00	0.00	0.00	0.00	0.00	0.31
MPI		(4)	(4)	(4)	(0)	(0)	(0)
	50	0.00	0.13	0.00	—	—	—
	75	0.25	0.25	0.50	—	—	—
	100	0.75	0.50	0.50	—	—	—
	125	0.00	0.13	0.00	—	—	—
PGM		(7)	(8)	(8)	(0)	(0)	(0)
	75	0.50	0.50	0.12	—	—	—
	100	0.50	0.50	0.88	—	—	—
AC		(4)	(4)	(4)	(7)	(0)	(8)
	80	0.00	0.00	0.00	0.00	—	1.00
	100	1.00	0.00	1.00	0.50	—	0.00
	150	0.00	1.00	0.00	0.50	—	0.00
ACP		(8)	(8)	(8)	(7)	(1)	(8)
	40	0.00	0.00	0.00	0.00	0.00	1.00
	60	0.00	1.00	0.00	0.00	1.00	0.00
	100	1.00	0.00	1.00	1.00	0.00	0.00
FUM		(12)	(12)	(12)	(7)	(1)	(8)
	62	0.00	0.00	0.00	0.00	0.00	0.56
	67	1.00	0.00	0.00	0.00	0.00	0.00
	88	0.00	0.00	0.00	0.00	0.00	0.44
	100	0.00	1.00	1.00	1.00	1.00	0.00
MDH		(12)	(12)	(12)	(7)	(1)	(8)
	70	0.00	0.00	0.00	0.00	0.00	0.56
	75	1.00	0.00	0.00	0.00	0.00	0.00

	90	0.00	0.00	0.00	0.00	0.00	0.44
	100	0.00	1.00	1.00	1.00	1.00	0.00
P3GDH		(12)	(12)	(12)	(7)	(1)	(8)
	30	0.00	0.00	0.00	0.00	0.00	0.50
	50	0.00	0.00	0.00	0.00	0.00	0.50
	67	0.00	0.00	1.00	0.50	0.50	0.00
	100	1.00	1.00	0.00	0.50	0.50	0.00
GPI		(8)	(8)	(8)	(7)	(1)	(8)
	80	0.00	0.00	0.00	0.00	0.00	0.38
	90	0.00	0.00	0.00	0.00	0.00	0.62
	100	1.00	1.00	1.00	1.00	1.00	0.00
G6PDH		(12)	(12)	(12)	(7)	(1)	(8)
	60	0.00	0.00	0.00	0.00	0.00	0.25
	75	0.00	0.00	0.00	0.00	0.00	0.75
	100	1.00	1.00	1.00	1.00	1.00	0.00
PEP-LA		(12)	(12)	(12)	(4)	(0)	(3)
	75	1.00	1.00	1.00	1.00	—	0.00
	100	0.00	0.00	0.00	0.00	—	1.00
TPI		(12)	(12)	(12)	(7)	(1)	(8)
	60	0.00	0.00	0.00	0.00	0.00	0.50
	80	0.00	0.00	0.00	0.00	0.00	0.50
	100	1.00	1.00	1.00	1.00	1.00	0.00
ALD		(12)	(12)	(12)	(0)	(0)	(0)
	100	1.00	1.00	1.00	—	—	—
SORDH		(12)	(12)	(12)	(0)	(0)	(0)
	100	1.00	1.00	1.00	—	—	—

netic incompatibility of the two species (Harrison 1990), a more robust sampling protocol than the one used in our study would be required to eliminate the possibility of localized hybrid zones or very subtle degrees of genetic introgression.

Hybridization between species with distinct genetic makeups is not uncommon in other attacine saturniids, although most occur in laboratory or otherwise unnatural settings. Not only are intrageneric hybrids possible within *Callosamia*, but intergeneric hybrids have been obtained from matings of *C. promethea* X *Hyalophora cecropia* and in crosses of all three *Callosamia* species X *Samia cynthia* (Drury) (Peigler 1978, Carr 1984). However, most of these hybridizations resulted in malformed or sterile offspring, presumably due to post-mating incompatibilities such as differences in chromosome numbers (Robinson 1971). Chemical differences in mating pheromones of attacine silk moths appear to play a minor role in maintaining reproductive isolation, since there are numerous reports of cross-attraction among the three *Callosamia* species and *Hyalophora cecropia* (Rau & Rau 1929, K. S. Johnson, unpubl. data).

In our study, *Hyalophora* was not useful for outgroup comparison due to the low number (one) of alleles shared with *Callosamia*, and the equal genetic differentiation between the three *Callosamia* species pairs sheds little light on their intrageneric relationships. On the other hand, the electrophoretic dissimilarity between *Callosamia* and *Hyalophora* is of interest because it suggests that these taxa may not be as closely related as presumed (Michener 1952). *Callosamia* is currently limited to the three taxa found only in North America, but the genus may be more closely allied with other attacine lineages, such as the Asiatic *Samia*. Patterns of host plant use support this relationship, as both *Samia* and *Callosamia* are unique within the Attacini in their ability to utilize magnoliaceous hosts (Stone 1991). *Hyalophora* occasionally have been reported to feed on plants in this family (primarily tulip tree) but larval survival on it is extremely low (Scarbrough et al. 1974, Manuwoto et al. 1985). Additional studies are needed to clarify the phylogenetic relationships among *Callosamia*, *Hyalophora*, *Eupackardia*, and *Samia*.

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EFFECT OF MALE ACCESSORY GLAND EXTRACTS ON INDUCTION OF OVIPOSITION IN THE GYPSY MOTH, *LYMANTRIA DISPAR* (LYMANTRIIDAE)

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ABSTRACT. In gypsy moths, *Lymantria dispar*, injection of saline extracts of male reproductive glands only slightly increased early oviposition by virgin females. Freshly mated females, ligated between the thorax and abdomen to prevent transmission of humoral factors, oviposited at the same time (37 to 53 min) as mated, nonligated, control females (59 min). Transplantation of spermathecae from either mated or senescent, actively-ovipositing unmated females into virgin moths did not elicit early oviposition. Females stimulated by insertion of a probe or injection of saline into the bursa copulatrix failed to oviposit. These data enhance previous findings by others suggesting that initiation of oviposition in gypsy moths is mediated neurally.

Additional key words: sex peptide, ligation, transplantation, spermathecaee.

Mechanisms for induction of oviposition differ among the Lepidoptera. In most cases, the presence of eupyrene sperm and/or testicular fluids in the female reproductive tract is needed to initiate oviposition. For *Hyalophora cecropia* (L.) (Saturniidae), the bursa copulatrix appears to secrete a bursa factor after being filled with sperm; oviposition is initiated by an undefined humoral mechanism (Riddiford & Ashenhurst 1973, Sasaki et al. 1983). A bursa factor also has been postulated for *Manduca sexta* (L.) (Sphingidae) (Sasaki & Riddiford 1984). However, in a follow-up study, Stringer et al. (1985) found that bursa transplants from mated females, which were expected to be humorally active, did not induce oviposition in virgins. They suggested other factors, such as juvenile hormone (JH), also may be needed and that the expanded bursa might transmit neural signals to the corpora allata to maintain the titer of JH. In the leek moth, *Acrolepiopsis assectella* (Zeller) (Acrolepiidae), spermatozoa must migrate to the spermatheca to stimulate oviposition (Thibout 1979). Eupyrene sperm and/or testicular fluids must be present (tissue not specified) for oviposition by larch bud moths, *Zeiraphera diniana* (Guenée) (Torticidae) (Benz 1969), and cabbage loopers, *Trichoplusia ni* (Hübner) (Noctuidae) (Karpenko & North 1973).

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There is ample evidence for both neural and humoral control of reproductive events in Lepidoptera as exemplified by studies of pheromone biosynthesis regulation in *Helicoverpa* (Noctuidae) (Teal et al. 1990, Christensen et al. 1991). The investigators suggested that pheromone biosynthesis-activating neuropeptide is released by efferent nerves acting on the terminal abdominal ganglion, which then signals the pheromone gland to synthesize pheromone. They also discovered a bursa factor that suppresses pheromone production through an undefined mechanism.

Males of several insects transfer factors to females during copulation that induce oviposition and inhibit receptivity to additional mating. Such substances have been reported in Diptera, Orthoptera, Lepidoptera, and Coleoptera (Leahy & Craig 1965, Leahy 1967, Nelson et al. 1969, Yamaoka & Hirao 1977, Morrison et al. 1982, reviewed by Gillott 1988). These factors are thought to be secreted by the accessory reproductive glands of the male. In Diptera, they are referred to as sex peptides based on the pioneering work by Fox (1956, Fox et al. 1959). Chen et al. (1988, Chen & Balmer 1989, Schmidt et al. 1993) have conducted the most extensive research on dipteran sex peptides and have been able to identify, characterize, and synthesize the sex peptides in three species of *Drosophila* (Drosophilidae). The sex peptides probably are transmitted through the bursa to the hemolymph and act on the brain to trigger oviposition (Chen 1991, Aigaki et al. 1991).

The physiological basis for induction of oviposition in gypsy moths, *Lymantria dispar* L. (Lymantriidae), is not fully understood. Adults are sexually mature upon eclosion and generally mate on the day of emergence (Leonard 1981). Females begin to lay an egg mass within 4 to 6 h after mating and complete the process within 3 days. If females have not mated within 5 days, they switch from virgin to mated behavior and spew some of their mature eggs before dying (Giebultowicz et al. 1990a). Although Giebultowicz et al. (1990b) suggest that sperm must be present in the spermathecae to initiate oviposition in gypsy moths, no studies specifically have examined whether humoral factors are involved.

Given prior research in J. Miller's laboratory on oviposition-stimulating substances (Spencer et al. 1992), the recent success in sex peptide characterization achieved by Chen et al. (1988, Chen & Balmer 1989), and the lack of comparable studies on the gypsy moth, we addressed the possibility that induction of oviposition in *L. dispar* might be influenced by a humoral factor from the male accessory glands. Discovery of substances promoting premature oviposition of unfertilized eggs might provide clues towards control of this economically important pest (Leonard 1981, Miller et al. 1994).

MATERIALS AND METHODS

Rearing. Gypsy moth egg masses, obtained from the USDA-APHIS facility at the Otis ANGB in Massachusetts, were surface-sterilized by soaking in 10% formalin for 1 h followed by a cold water rinse for 1 h. Insects were maintained at 24±2 C, 55±5% RH, and a L:D 16:8 h cycle. Groups of 10 newly emerged larvae were placed into 60 ml clear plastic cups and reared on a high wheat germ diet (Bell et al. 1981). During the second instar, individual larvae were transferred into cups with sufficient food for growth to pupation. Pupae were sexed according to size (females are approximately 50% larger than male pupae). Female pupae were placed into a group cage and males were placed individually into 150 ml plastic cups until adult eclosion. Since gypsy moths are sexually mature upon eclosion and because virgin females begin senescent oviposition at about 5 days old, experiments were conducted on males and females 0–2 days old, unless noted otherwise.

Ligation. Newly eclosed female moths (less than 18 h old) were ligated 1, 15, 30, 60 and 180 min after the onset of mating to disrupt humoral communication between the abdomen and head. A 5-0 nylon suture was looped around the thoracic-abdominal junction of female moths, then tightened sufficiently to stop hemolymph flow but not enough to sever the ventral nerve cord. In positive (normally mated) and negative (virgin) control moths, ligatures were applied but not tightened. Anesthesia was not used. The ligature was not tightened prior to copulation (at 0 min) because a preliminary experiment suggested that it reduced either a female's willingness to copulate or her attractiveness to the male. We judged it unlikely that any humoral factors would be released into the hemolymph from the bursa and be transported out of the abdomen during the first minute of copulation. All moths were injected in the abdomen with 0.5–1.0 ml India ink (undiluted) at the end of the experiment to identify moths with incomplete ligations, and some were injected immediately after ligation to measure failure rate of ligation. Preliminary tests showed that India ink readily circulated through all three tagmata of nonligated females.

Extract preparation and injection. Male whole reproductive tract, accessory gland/ejaculatory duct complex, vas deferens/seminal vesicle complex, and testis were dissected from freshly frozen moths and placed into a microcentrifuge vial containing Ringer's saline kept on ice. Extracts were prepared by homogenizing the tissues for 20–30 seconds with an ultrasonic probe, setting the tuner 3 and the power 35 (Blackstone Ultrasonics Inc., Sheffield, Pennsylvania), then centrifuging at 6000 g for 10 minutes. The concentration of the supernatant was adjusted so that 7.0 μl of extract corresponded to 1 male equivalent of tis-

sue. Extracts were used immediately or removed and stored for up to 5 days at –20°C before use. Female moths were anesthetized with CO_2 for 2 min, then injected with a 30 gauge needle into the ventrolateral side of the pleuron between abdominal segments A2 and A3.

Surgical procedures. Female moths were anesthetized with diethyl ether for 30–60 sec prior to surgery. To examine whether isolated abdomens would oviposit, female moths were allowed to mate, then their abdomens were resected at 1, 3, 5, and 7 h after the onset of mating. For tagmatal isolation studies, either the thoracic-abdominal junction or the head-thorax junction was tied off with a suture and resected anteriorly. Since the spermatheca is the target organ of sperm following dissociation of the sperm in the bursa copulatrix and oviposition is markedly reduced in females without a spermatheca but not in females without a bursa copulatrix (Giebultowicz et al. 1990b), spermathecae were transplanted to determine whether they were humorally active. One-day-old virgin females received a spermathecal transplant from one of three donor types: 1-day-old mated, ovipositing females; senescent, ovipositing virgins; 1-day-old nonovipositing virgins. For the transplantation study, spermathecae were removed from donor moths through an incision on the ventral side above the bursa opening. These were transplanted immediately into virgins through a scalpel puncture anterior and lateral to the bursa. The sham control surgery consisted of a scalpel puncture followed by forceps insertion. All wounds were sealed with melted beeswax.

Quantification of oviposition. Since oviposition in normally mated females generally begins between 3–5 h postmating, all treatments were administered between 0 and 7 h after initiation of copulation to maximize the probability of causing a behavioral response. In the ligation and isolation experiments, ovipositional activity was monitored continuously on the first day and daily thereafter. In other experiments, females were examined daily to record the onset of oviposition. Egg masses were weighed to an accuracy of 0.1 mg.

RESULTS

Effect of ligation on oviposition. To determine whether the presence of a ligature would adversely affect mating and oviposition, the time ligated females remained *in copulo* was compared to that of normally mated females. There were no significant differences in copulating time among ligated females compared to nonligated females, regardless of when females were ligated (Table 1). Although females ligated at 30 min tended to disengage during the ligation procedure or soon after, there was no apparent effect on other parameters measured. Overall, ligation had little effect on duration of copulation.

TABLE 1. Gypsy moth mating, oviposition and egg weight at 3 days following ligation. Newly eclosed females were ligated at the times indicated after the onset of mating. In positive and negative control moths, ligatures were applied but not tightened. Results presented as means ± standard deviation. Within each column, treatment means with the same letter are not significantly different ($p<0.05$) using Student-Newman-Keuls test (Ott 1988) for multiple comparison of means following analysis by a general linear model. Time ligated refers to time after initiation of copulation.

Treatment	N	Mean copulation time (min)	Elapsed time to oviposition (h)	Egg mass weight (mg)
Time ligated				
1 min	7	51 ± 14 [a]	14 ± 26 [a]	522 ± 275 [a]
15 min	5	53 ± 21 [a]	10 ± 10 [a]	579 ± 88 [a]
30 min	5	37 ± 13 [a]	4 ± 2 [a]	568 ± 235 [a]
60 min	4	46 ± 17 [a]	5 ± 3 [a]	663 ± 100 [a]
180 min	3	53 ± 17 [a]	5 ± 2 [a]	548 ± 40 [a]
Control				
mated, not ligated	9	59 ± 21 [a]	6 ± 3 [a]	712 ± 107 [a]
virgin, not ligated	5	—	72 ± 1 [b]	15 ± 13 [b]
virgin, ligated	7	—	57 ± 26 [b]	101 ± 200 [b]

The effect of ligation on oviposition activity in moths was investigated by measuring elapsed time from initiation of mating to initiation of oviposition and the weight of the egg mass at three days posttreatment. Mated moths in both the ligated and nonligated groups (Table 1) had similar elapsed times to oviposition and similar egg mass weights. For moths ligated at 1 and 15 min, oviposition appeared to be delayed somewhat compared to later ligation times. However, in each case there was one female per group that oviposited much later than the rest. If those data are removed from the analysis, elapsed time to oviposition is 4±3 h and 6±4 h for the 1 min and 15 min ligation, respectively. Virgin moths placed in oviposition cages at the same time as mated moths took significantly longer to begin ovipositing; only half of the females had laid any eggs at the end of three days, which is characteristic of senescent virgins. The results for ligated virgins were more variable than unligated virgins because two moths in the ligated group began ovipositing late in the first day whereas the other five began at around 72 h. Perhaps the ligatures had some effect on inducing early oviposition but not to the extent that mating does. In both virgin groups, mean egg weights were significantly lower as expected (Table 1).

Several moths with incomplete ligations were not included in the above analyses. However, in effect, they served as parallel controls revealing the effect of applying the ligature at each time period without blocking hemolymph flow. Mean latency to oviposition and mean egg

TABLE 2. Oviposition and egg weight of gypsy moths with complete and incomplete ligations. Moths with incomplete ligations are shown next to those with complete ligations to illustrate the effect of ligation without blocking hemolymph exchange. Treatment means with the same letter are not significantly different at $p<0.05$ by SNK (see Table 1). Time ligated refers to time after initiation of copulation. Asterisks indicate samples of $n=1$.

	Hours to oviposit		Egg weight (mg)	
Treatment	Complete ligation	Incomplete ligation	Complete ligation	Incomplete ligation
Time ligated				
1 min	14	7	523 [a]	712 [a]
15 min	10	6	579 [a]	667 [a]
30 min	4	7	568 [a]	698 [a]
60 min	5	2*	663 [a]	698 [a]
180 min	5	7	548 [a]	595 [a]
virgin, ligated	57	49*	101 [b]	24 [b]

weights were not different among mated moths with complete versus incomplete ligations at all time periods (Table 2).

Injection of male reproductive gland extracts. Normally mated (positive control) females oviposited sooner and with more complete formation of the egg mass than any of the treated groups (Fig. 1). Virgins injected with one male tissue equivalent oviposited at approximately the same rate as virgins injected with the same volume of saline only. Untreated virgins (negative control) began egg deposition by day 4 as expected. The ovipositional response of moths receiving injections fell between the positive and the negative controls but most closely resembled the saline control.

Transplantation of spermathecae from ovipositing females into nonovipositing females. Transplant recipient virgins in all groups oviposited at approximately the same rate as sham transplanted control virgins, which oviposited later than normally mated females (Fig. 2). Both mated and transplanted females initiated oviposition sooner than untreated virgins, but this effect was due to the surgery as evidenced by egg output from sham transplanted females.

Effect of abdomen isolation and decapitation on oviposition. None of the isolated abdomens ($n=3$ for each time period) laid eggs during the three days following resection although they appeared to be alive. In the 5 and 7 h groups, 2 of 3 moths had begun oviposition prior to resection of the abdomen but did not continue laying eggs after isolation. To further evaluate this phenomenon, moths were decapitated 1 h ($n=2$) and 3 h ($n=3$) after initiation of copulation so that the thorax and

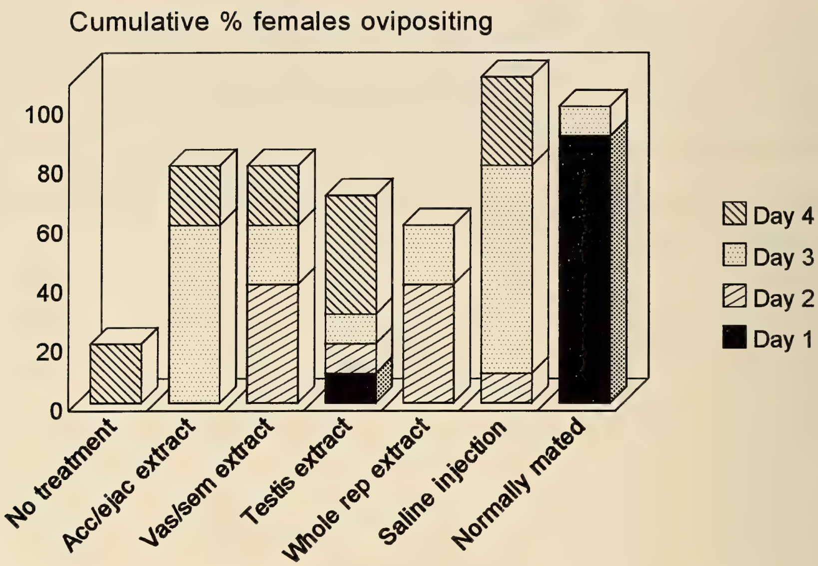

FIG. 1. Gypsy moth oviposition through 4 days following injection with extract of male reproductive tissue. Extracts injected into virgin females were prepared from: (a) accessory gland/ejaculatory duct; (b) vas deferens/seminal vesicle; (c) testis; and (d) whole male reproductive tract. Negative controls included untreated and saline injected virgins; the positive control consisted of normally mated females. N=10 for all treatments.

abdomen were intact. Although 1 moth in the 3 h group began laying eggs prior to treatment, none of the moths oviposited following decapitation.

Effect of bursa stimulation. Females were stimulated artificially by introducing a probe and injecting saline into the bursa. Glass rods (0.2 mm diam., 10 mm long) were inserted into the bursa and either gently manipulated for 2 min and removed or left in place for the duration of the experiment. Oviposition by moths at 5 days posttreatment was no greater than that by virgins handled the same way but without rod insertion. In another experiment, injection of 60–70 ml of Ringer's saline into the bursa through fine-tipped, polyethylene tubing also did not induce oviposition greater than that observed in negative controls.

DISCUSSION

If oviposition in gypsy moths were induced by a male-derived humoral factor acting on the brain, then early ligation should prevent transmission of the factor, causing a delay in egg laying. Similarly, late ligation should have no effect and treated females should behave as if they were normally mated. In these studies, ligated females oviposited

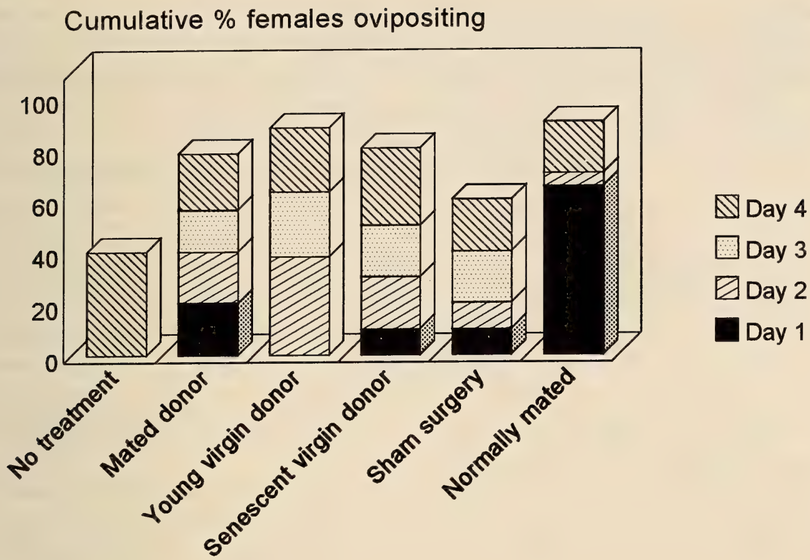

FIG. 2. Gypsy moth oviposition through 4 days following transplantation with spermathecae from various donors. Virgin gypsy moths received a spermatatheca from one of 3 donor types: (a) 1-day-old mater, ovipositing female; (b) senescent, ovipositing virgin; and (c) 1-day-old non-ovipositing virgin. Negative controls included untreated and sham transplanted virgins; the positive control consisted of normally mated females. N=8–20 per treatment.

at the same time as nonligated females and both groups produced comparable egg masses regardless of when a thoracic-abdominal ligature was applied (Table 1).

At best, the data in Fig. 1 suggest that females injected with semen- and sperm-containing extracts (the three middle groups in the figure) began oviposition a day or two earlier than those receiving accessory gland extract or saline. Injections of gypsy moth male reproductive gland extracts, including the highly secretory upper vas deferens (Riemann & Giebultowicz 1991), did not stimulate oviposition in virgin females comparable to the mated rate. Studies of male paragonial gland extracts have shown these methods to be successful for demonstrating humorally active, male-produced oviposition factors in Diptera (Leahy & Craig 1965, Riemann & Thorson 1969, Morrison et al. 1982, Chen et al. 1988). Moreover, in *Bombyx mori* (L.) (Bombycidae) injection of a saline or water extract of whole reproductive tract stimulated oviposition in virgin females (Yamaoka & Hirao 1977) whereas extract of abdomen (minus reproductive tract, alimentary canal and malpighian tubules) produced only a minor effect. In addition, whole reproductive extract

added to *in vitro* preparations containing the terminal abdominal ganglion increased the spontaneous firing of associated motoneurons. Yamaoka and Hirao (1977) provided evidence in Lepidoptera for a humorally transported, oviposition-stimulating component in male reproductive tract that also appears to exert a neural effect.

Our experiments involving transplantation of spermathecae from actively ovipositing females into fecund virgins elicited the same ovipositional response as transplants from nonovipositing virgins. Giebultowicz et al. (1990b) likewise reported no effect when transplanting spermathecae from females 1.5 to 3 h after mating into virgins.

The current tagmatal isolation studies suggest that oviposition is not solely controlled by the abdominal or thoracic ganglia. The head appears to be important in initiating oviposition since mated, decapitated moths did not oviposit but intact, ligated moths did. Perhaps the command to begin egg laying originates in the brain.

Several investigators have postulated that in Lepidoptera the events resulting in decreased pheromone production also may initiate oviposition (Thibout 1979, Sasaki et al. 1983, Sasaki & Riddiford 1984, Stringer et al. 1985, Giebultowicz et al. 1990a). Giebultowicz et al. (1991) showed that a 2 min stimulation of the bursa either by male genitalia or by a thin glass rod caused a temporary decline in gypsy moth pheromone production; the spermathecae needed to be present for up to 5 h after mating to result in permanent suppression of pheromone production and calling behavior. In our studies, mechanical stimulation of the bursa failed to elicit premature oviposition by virgins.

Giebultowicz et al. (1990b, 1991) suggested that stretch receptor nerves in the spermathecae of *L. dispar* mediate an ovipositional response after the spermathecae have filled with sperm. In their studies of females mated to males kept in constant light as pharate adults, a spermatophore was formed in the bursa but few or no sperm migrated to the spermathecae and females failed to lay eggs. This is similar to the work of Klatt in 1920 (referenced in Benz 1969) who showed that castrated *L. dispar* males, which produced spermatophores without sperm, did not stimulate females to oviposit. Both of these studies concur with a 1952 study by Behrenz (referenced in Giebultowicz et al. 1990b) who showed that oviposition was reduced in *L. dispar* females in which the spermathecae had been removed or ligated to prevent sperm migration.

Given these earlier findings and our lack of strong evidence for humoral mediation involving the brain, we agree with Giebultowicz et al. (1990b, 1991) that sperm interacting with the spermatheca is the predominant inducer of oviposition in this laboratory strain of the gypsy moth. However, it remains unclear whether the sperm act humorally or neurally. Giebultowicz et al. (1990b, 1991) suggested that stretch recep-

tors surrounding the spermatheca send a signal to initiate oviposition, either through a neural or neurohumoral sequence. An equally plausible explanation is that sperm receptors lining the spermathecae release a paracrine factor that acts independently of or in concert with nervous stimuli. Neither of these hypotheses explains the onset of oviposition by senescent virgins.

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GENETICS OF A "ZEBRA" PIGMENT MUTATION IN THE LARVAE OF *DANAUS PLEXIPPUS*, L. (NYMPHALIDAE: DANAINAE)

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ABSTRACT. We report a mutation in monarch butterflies that results in a lack of yellow pigment in larvae, pupae and eggs. Genetic studies reveal that this phenotype is caused by a recessive autosomal allele with normal Mendelian segregation. We did not detect an effect on butterfly size or asymmetry, but mutant individuals of both sexes appear to suffer lower reproductive success than normal individuals. We hypothesize that the mutants are unable to sequester carotenoids from their larval host plants.

Additional key words: carotenoids, pigmentation.

Lepidopteran coloration plays important roles in camouflage, warning, mimicry, and mate recognition, and knowledge of the genetic and biochemical mechanisms of pigmentation will lead to greater understanding of evolution in this group. Here we report a mutation in the monarch butterfly, *Danaus plexippus* L. (Nymphalidae), that affects egg, larval, and pupal pigmentation. This mutation shows simple Mendelian inheritance, and we hypothesize that it is caused by a recessive autosomal allele that prevents carotenoid sequestration in larvae.

MATERIALS AND METHODS

In May 1994, we received 30 monarch pupae from Tennessee to use as parents of butterflies for several experiments. These were all the offspring of three wild females, but the parentage of individuals was not known. All of the Tennessee pupae had normal appearance, as did the adults that emerged from them. Adults were kept in glassine envelopes for four days after emergence, then put into a large outdoor screen cage,

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where eleven pairs mated. Mated females were kept in individual outdoor cages with cuttings of *Asclepias syriaca* L. (Asclepiadaceae), and between 75 and 150 eggs from each were reared to adulthood. Larvae from each female were kept in separate screen cages in a screened room where they experienced ambient temperatures and photoperiod. They were fed fresh cuttings of *A. syriaca* daily. One day after experimental adults emerged, we weighed them to the nearest 0.01 mg on a Mettler analytical balance, and measured the length of both forewings to the nearest 0.01 mm with a vernier caliper.

RESULTS

Zebra phenotype. One of the eleven F_1 sibling broods from the Tennessee butterflies contained larvae that lacked the yellow stripes characteristic of normal monarch pigmentation. Because of their alternate white and black stripes, we called this unusual phenotype "zebra." Other larvae in the brood were normally colored. Zebra pupae were blue-green, and their metallic spots silver. Siblings with a normal phenotype produced typical green pupae with gold spots. We detected no differences between zebra and normal adults, but zebra females laid white eggs, while typical monarch eggs are cream-colored.

We compared the size (mass and right forewing length), and forewing asymmetry (the absolute value of the difference between the right and left forewing lengths) of zebra individuals with other experimental butterflies. Comparisons were made both between sibships (that contained and did not contain zebra individuals) and within zebra sibships. These two comparisons were made because there are sometimes family effects on size (Oberhauser 1989, and unpubl. data) that could confound effects of the zebra genotype. We analyzed males and females separately, since females were slightly smaller than males. The results of two-tailed t-tests of these comparisons are summarized in Table 1. There were no mass or asymmetry differences between any of the groups, but the family that contained zebras had significantly shorter forewings than the rest of our butterflies. This was true of both males and females. Within this family, however, forewing lengths of zebra individuals were not significantly different from their normal siblings.

We have not carried out detailed studies of life history characteristics of zebra individuals, but our observations suggest that there are fitness consequences of this mutation. Zebra males rarely mate when put into cages with females, and are more difficult to hand-pair than normal captive males. Zebra females lay fewer eggs than normal females and a higher proportion of their eggs fail to hatch.

Transmission of the zebra trait. The proportions of normal and zebra individuals in the initial zebra brood and the likelihood that their

TABLE 1. Size and asymmetry comparisons of zebra to normal larvae of *Danaus plexippus*. A, males. B, females. All measurements compared using 2-tailed two sample t-tests. Measurements given are group means followed by one SD (in parentheses).

	N	mass (mg)	right forewing length (mm)	abs.value forewing asymmetry (mm)
A: males				
zebra family	36	525.76 (48.10)	50.88 (1.47)	0.28 (0.21)
all others	341	518.00 (55.24)	51.98 (1.89)	0.32 (0.35)
p		0.418	0.003	0.514
zebra individuals	12	531.20 (36.20)	51.15 (0.91)	0.25 (0.21)
normal siblings	24	523.03 (53.58)	50.68 (1.78)	0.31 (0.21)
p		0.618	0.407	0.476
B: females				
zebra family	28	480.00 (52.54)	50.20 (1.89)	0.36 (0.29)
all others	404	479.71 (58.46)	51.39 (2.17)	0.32 (0.36)
p		0.958	0.008	0.560
zebra individuals	10	480.49 (59.50)	50.22 (2.30)	0.32 (0.24)
normal siblings	18	479.13 (39.90)	50.16 (1.14)	0.39 (0.31)
p		0.947	0.939	0.503

parents were siblings suggested that the trait was caused by a recessive allele. To test this, we set up matings among zebra adults, their siblings with normal pigmentation, their offspring, and non-siblings from our experimental stock. All matings that involved zebra males were hand-paired, as were about half of the other matings (we hand-pair butterflies often when we want specific individuals to mate, and have no evidence that this affects mating success). We reared offspring from all crosses as described above, with the exception of those in Table 2f. These crosses were done in our laboratory in the fall and winter, and the larvae reared on *A. currasavica* (Asclepiadaceae) or *Cynachum laeva* (Asclepiadaceae) grown in a greenhouse.

Table 2 summarizes the results of these crosses, and gives the expected proportion of offspring with the zebra phenotype from each type of cross. Expected values were calculated as follows: We called the recessive zebra allele *z*, and the dominant, wild-type allele Z. Thus the genotype of a zebra individual is hypothesized to be *zz*, and a normal individual ZZ or *Zz*. A *Zz* x *Zz* cross should result in a brood that contains 1/4 ZZ, 1/2 *Zz* and 1/4 *zz* individuals. Two-thirds of zebra x zebra sibling matings from a brood with this genotype ratio should be *zz* x *Zz*, and thus produce 1/2 zebra individuals, while one-third should be *zz* x ZZ and produce only individuals with a normal phenotype. Crosses between

TABLE 2. Phenotypic ratios of the zebra trait in laboratory crosses in *Danaus plexippus*. Zeb=zebra individual, Sib=normal sibling of zebras, NS=individual that is a non-sibling of zebra family, F_2=offspring of Zeb x NS cross; letters followed by the same superscript represent the same individual (all other individuals are unique). Confidence intervals when proportion of zebras = 0 or 1 calculated according to Blythe and Still (1978).

	♀ x ♂ phenotypes	# zebra larvae	# normal larvae	observed proportion zebras	95% CI for proportion zebras	expected proportion zebras
a	initial cross	45	105	0.30	0.23 – 0.37	0.25
b	Zeb x Zeb	45	0	1.0	0.902 – 1.0	1.0
c	Zeb x Sib[1]	0	10	0	0 – 0.38	2/3 broods 0.5, 1/3 0
	Zeb x Sib[1]	0	9	0	0 – 0.43	
	Sib x Zeb[2]	0	72	0	0 – 0.063	
	Sib x Zeb[2]	0	46	0	0 – 0.096	
d	Sib x Sib	15	36	0.29	0.17 – 0.41	4/9 broods 0.25, 5/9 0
	Sib x Sib	14	24	0.37	0.22 – 0.52	
e	NS x Zeb[3]	0	97	0	0 – 0.048	most broods 0
	NS x Zeb[3]	0	74	0	0 – 0.062	
f	F_2 x F_2	41	133	0.24	0.21 – 0.27	0.25
	F_2 x F_2	26	77	0.25	0.17 – 0.33	

two zebra siblings should only result in any zebra offspring if both parents are *Zz*; this should be true 4/9 of the time. Depending on the contribution of the three wild females to our initial stock, from 1/2 (if the female containing the zebra gene [or mated to a male containing the gene] produced all thirty individuals) to 1/30 (if this female only produced a single individual) of our stock are expected to have been zebra heterozygotes. If all three females contributed equally to the stock, we would expect 1/6 of this stock to be zebra heterozygotes. Thus it is impossible to calculate precisely the expected outcomes of matings that include non-siblings from our initial stock.

The initial zebra brood, which we assumed resulted from a *Zz* x *Zz* mating, contained 32% zebra larvae (Table 2a). The matings summarized in Table 2b-2e were either between siblings from this brood or one individual from this brood and a non-sibling. All offspring from a mating between two zebra parents (*zz* x *zz*) were themselves zebras (Table 2b). All of the offspring from crosses between zebras and their normal siblings (*zz* x Z_) were normal (Table 2c). Two crosses between normal siblings from the initial mating (Z_ x Z_) resulted in broods that contained both larval types (Table 2d). Crosses between zebras and non-siblings resulted in normal larvae (Table 2e).

We used F_2 offspring from the crosses between zebras and unrelated individuals represented in Table 2e for the matings in Table 2f. While all of these individuals had a normal phenotype, they should have been

heterozygotes. As predicted, presumed *Zz* x *Zz* matings resulted in broods that contained both types of larvae (Table 2f).

The 95% confidence intervals for the percentages of zebra larvae in crosses between presumed heterozygotes (Table 2a, 2d and 2f) included 25%, as predicted by our hypothesis. The bias toward higher than expected percentages of zebras in crosses represented in Table 2a and 2d could be explained by our summer rearing technique. We keep individual broods together, but in some cases larvae escape from their cages or wander away while we change their plants. Larvae of unknown origin are discarded so that we do not mix broods. Wandering zebra larvae were not discarded, because their origin was usually clear. The F_2 crosses shown in Table 2f were done in the fall, when we keep larvae on potted plants, thus reducing the likelihood of escape; in both of these crosses the proportion of zebra larvae was close to the prediction.

The fact that all of the progeny from crosses in Table 2c (between three normal individuals and their zebra siblings) were normal suggests that the three normal siblings chosen for these matings were all *ZZ*. The probability of three *ZZ* individuals being drawn for these matings is 0.037 (0.333^3), given our genetic hypothesis. Even though two of these crosses resulted in few viable offspring, *zz* x *Zz* crosses should result in broods that are half zebras, and neither of the 95% confidence intervals for these small broods included 50%.

Both of our crosses between normal siblings produced mixed broods (Table 2d), suggesting that both crosses were *Zz* x *Zz*. The probability of this occurring is 0.197 (0.667^4).

Sex ratios in all broods did not differ significantly from 50% (data not shown), suggesting that there is no sex linkage of this trait.

DISCUSSION

Our results support the hypothesis that the zebra trait in monarchs is caused by a recessive autosomal allele. One successful cross between two zebra individuals resulted in the only brood that consisted solely of zebra individuals (Table 2b), crosses between zebra and non-siblings resulted in broods that all appeared normal (Table 2e), and crosses between their presumed heterozygote progeny resulted in broods that had one quarter zebra offspring (Table 2f). There was no sex bias in the transmission of the trait.

We should note that crosses represented in Table 2c between zebra individuals and three of their siblings with normal phenotypes are inconsistent with the hypothesis; two thirds of the normal siblings are expected to be heterozygous carriers, yet we saw no zebra individuals in any of these broods. The only explanations that fit the rest of our results are that, against statistical odds, we chose three homozygous normal in-

dividuals for these matings, or the small broods from two matings misrepresent their possible phenotypes.

We have not studied the biochemical mechanisms that are responsible for the lack of yellow pigment in our zebra larvae and pupae, and their eggs. However, based on studies of larval pigmentation in other Lepidoptera, we hypothesize that these larvae do not sequester the carotenoids they obtain from their host plant. Carotenoids (carotenes and xanthophylls) are often responsible for yellow coloration in insects, including Lepidoptera (e.g., Chapman 1982, Kayser 1985). When the yellow carotenoids are combined with blue bile pigments, they result in the green colors that are common in many lepidopteran larvae and pupae (Feltwell 1978, Rothschild 1978, Kayser 1985). Although we have found no reported cases of mutant larvae lacking yellow coloration, other workers have implicated autosomal recessive genes in the blue-green coloration of larvae that are normally green (*Colias philodice*, Gerould 1921, Hoffman & Watt 1974; *Hyalophora cecropia*, Waldbauer & Sternburg 1972; and *Papilio memnon*, Clarke & Sheppard 1973). Phenocopies of these mutants can be produced by feeding larvae artificial diets lacking carotenoids (Clarke 1971, Valadon et al. 1975, Feltwell 1978, Rothschild 1978). In addition, the larvae of other Danainae raised on carotenoid-free diets produced pupae in which the gold sheen was silver (Rothschild et al. 1978), and *Pieris brassicae* larvae reared on diets that contained almost no carotenoids laid white, but fertile eggs (Rothschild 1978).

Hoffman and Watt (1974) demonstrated that the hemolymph of normal *Colias philodice* larvae contains a yellow pigment, presumably the carotenoid lutein, bound to a protein with a molecular weight of about a million daltons. This carotenoid/protein complex was absent in the hemolymph of blue-green mutants. Bergman and Chippendale (1992) demonstrated that carotenoids in larvae of the southwestern corn borer, *Diatraea grandiosella*, are transported in the hemolymph by lipophorin. It is likely that a mutation in the gene coding for this or a similar protein is responsible for the lack of yellow pigment in our zebra line and other mutant lepidopteran lines described above.

In addition to their role in coloration, carotenoids have two well-documented functions that could be implicated in the lower fitness that we observed in zebra monarchs. These include protecting cells from photooxidative damage caused by the absorption of visible and near UV light (Krinsky 1979), and serving as precursors for the formation of visual pigments that are needed for normal vision (Kayser 1985). Rothschild (1978) noted that adult *Pieris brassicae* reared on carotenoid-deficient diets were rather inactive, and suggested that this was due to defective vision. This could explain the low mating ability of zebra males in cages,

but is unlikely to be responsible for our lack of success in hand-pairing them. It is also possible that they had suffered photo-oxidative damage.

It is interesting that there are no clear effects on adult size associated with the trait. We suspect that the shorter winglength in the family that produced the zebras is unrelated to the trait, since it is not more pronounced in zebra individuals themselves, but it is possible that heterozygous individuals also are affected in an unknown manner.

The degree of fluctuating asymmetry (FA), or small, random deviations from bilateral symmetry in morphological traits, has attracted a great deal of recent attention as an indicator of overall fitness in animals (e.g., Parsons 1992). Many traits can be measured to indicate the symmetry of an organism, but the choice of wing length is common to many studies of FA in insects (e.g., Thornhill 1992, Harvey & Walsh 1993, Ueno 1994). FA is a measure of developmental stability, and can result from both environmental and genomic stresses (Parsons 1992). In some insects, homozygosity of rare major genes results in increased FA, presumably because this causes major genetic perturbations (Reeve 1960, Clarke & McKenzie 1987). The lack of greater FA in the forewing lengths of zebra monarchs indicates that some genes that decrease fitness may have no effect on the developmental processes that affect wing symmetry.

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CATERPILLAR LEAF FOLDING AS A DEFENSE AGAINST PREDATION AND DISLODGMENT: STAGED ENCOUNTERS USING *DICHOMERIS* (GELECHIIDAE) LARVAE ON GOLDENRODS

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ABSTRACT. Leaf tying and folding are common habits among caterpillars, with a variety of potential functions ranging from alteration of leaf chemistry and microclimate to protection from predators and dislodgment. However, predators may use leaf ties and folds as a cue to caterpillar presence, in which case such refuges could be a liability. I evaluated the protective function of leaf folding in two species of caterpillars (*Dichomeris* spp.) feeding on goldenrods (*Solidago* spp.). Staged encounters confirmed that common field and forest predators (ants and three species of spiders) paid little if any attention to leaf refuges (silk mats of early instar larvae and folds of older larvae), and that they could not penetrate refuges to attack larvae inside. These predators did kill caterpillars outside leaf refuges, although they often overlooked small or less active larvae and had relative difficulty capturing the largest larvae. Leaf refuges also prevented larvae from being dislodged during simulated wind or mammal disturbance to their host plant.

Additional key words: ant, leaf fold, leaf tie, *Solidago*, spider.

Leaf rolls, folds, and ties have long been assumed to protect caterpillars against predators (Frost 1959), and recent experimental evidence confirms that leaf refuges improve caterpillar survivorship specifically in the presence of birds, ants, or wasps (Fowler & MacGarvin 1985, Heads & Lawton 1985, Damman 1987, Atlegrim 1989, 1992, Vasconcelos 1991; but see Ito & Higashi 1991) or more generally where predation and perhaps dislodgment from the host are serious risks (Cappuccino 1993). But leaf refuges can also serve as a cue to predators, and the few detailed observations in the literature suggest that they are not always effective protection. A variety of birds (Robinson & Holmes 1982, Heinrich & Collins 1983, Greenberg 1987) and some wasps (Steiner 1984) open leaf folds to reach the occupants. Other arthropod predators may be attracted to caterpillar leaf refuges as resting sites (Frost 1959, Danthanarayana 1983).

This paper reports observations of some protective functions of leaf refuge-making against predation and dislodgment in the gelechiid caterpillars *Dichomeris leuconotella* (Busck) and *D. bilobella* (Zeller), both of

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which fold leaves on *Solidago* and *Aster* species (Asteraceae) (Hodges 1986, Loeffler 1994). Invertebrate predators are common on these plants. The vast majority of potential *Dichomeris* predators found in surveys of field and forest goldenrods near Ithaca, New York were spiders, followed by ants and occasional reduviids, nabids, cantharids, syrphid larvae, harvestmen, lacewing larvae, asilids, and predaceous mites (Loeffler 1992, 1993; mites may have been more common than observed in these surveys because of their small size, but they are probably relatively ineffective predators of most *Dichomeris* larvae for the same reason). Dislodgment is also a threat to the caterpillars because goldenrod ramets, especially those in forests, are frequently bent or knocked down by falling branches or passing mammals (Loeffler 1992). Caterpillars falling from a host plant often have difficulty locating another, especially where hosts are scattered (Dethier 1959a, 1959b, 1987, Jones 1977, Cain et al. 1985, Damman 1991).

MATERIALS AND METHODS

The caterpillars and their refuges. *Dichomeris leuconotella* and *D. bilobella* larvae differ in their phenology and habitat preferences (Loeffler 1994). In central New York, *D. leuconotella* larvae hatch in late July or early August from eggs laid singly on leaf undersides. First and second instars construct elongate silk webs, up to several times their body lengths. They feed beneath these webs and also exit the refuge at any time of day or night to feed within a few mm of either end (Loeffler 1994). By the third instar, caterpillars are able to pinch or fold the leaf, after which they feed mainly inside the fold. Each caterpillar constructs one to several refuges between hatching and early October, at which time it leaves the plant as a 3-4 mm long third or fourth instar to overwinter in dead leaves on the ground. In late April or May, the caterpillars crawl from the leaf litter onto new goldenrod ramets and begin several weeks of rapid growth accompanied by frequent refuge changes. Sixth (sometimes seventh) instar caterpillars pupate in leaf folds in mid- or late June, and adults fly in late June and early July (Loeffler 1994).

Dichomeris bilobella adults lay eggs in summer, but larvae do not appear on the plants until the following spring. They develop rapidly and conclude their sixth and final instar about two weeks later than larvae of *D. leuconotella*, at a similar size (ca. 16–17 mm). Their leaf folds are much tighter than those of *D. leuconotella*, being barely wide enough to accommodate the larva. *Dichomeris bilobella* is generally more common in forests than in fields, whereas *D. leuconotella* is restricted to open habitats (Loeffler 1994).

Predator trials. I exposed *Dichomeris leuconotella* and *D. bilobella* caterpillars of various sizes to typical oldfield predators (ants) and the

most common forest predators (theridiid, salticid, and araneid spiders) to compare predators' abilities to catch larvae with and without leaf refuges. Voucher specimens of the predators and of *Dichomeris leuconotella* and *D. bilobella* are deposited in the Cornell University Collection under Lot No. 1209. Additional voucher specimens of *Dichomeris leuconotella* and *D. bilobella* are deposited in the U. S. National Museum.

The oldfield predators, *Formica* sp. (of a taxonomically difficult entity within the *Formica fusca* complex, W. L. Brown, Jr., pers. comm.), are large, black, mound-building ants common in many fields near Ithaca, New York. In spring of 1987 and 1988, I allowed 15 fifth instar and 15 sixth (final) instar field-collected caterpillars of each *Dichomeris* species to fold leaves on goldenrod stem tops in vials of water. To assure leaf thicknesses and shapes representative of the variety of *Solidago* species available in nature to *Dichomeris*, I put one third of the larvae in each age group on *Solidago rugosa* Aiton collected from oldfields; one third on *S. rugosa* collected from forest; and one third on the forest species *S. caesia* L. These three types of goldenrod have, respectively: small thick hairy leaves; large, thin, somewhat less hairy leaves; and large, thin, smooth leaves. I ran the final instar *D. leuconotella* trials two weeks ahead of the final instar *D. bilobella* trials, because *D. leuconotella* matures earlier than *D. bilobella*.

After each caterpillar had fully completed its leaf fold atop its respective stem top, I stood the stem top in its vial on a *Formica* mound and allowed ants to crawl over the leaves. I recorded each time that an ant crawled on the leaf with the refuge and larva as an "encounter." After at least six "encounters," I removed the caterpillar from its refuge and returned it to the mound on a second goldenrod stem top, with no refuge. Observations were repeated on this second stem top until six "encounters" had occurred or until the ants had seized the caterpillar or caused it to drop from the stem top. I completed observations on each caterpillar before beginning trials with the next one. In this way, ants were presented with a long alternating sequence of larvae with refuges and larvae without refuges, which should have prevented any effects of order of presentation on ant behavior.

In September, 1987 I repeated this procedure with six third and fourth instar *D. leuconotella* larvae, and I ran additional trials indoors in jars, with 3-6 recently-collected ants per jar, after cold weather made the ants inactive outside. In the indoor trials, where each larva was to be placed with a specific, confined set of ants, effects of order of presentation were of concern. I therefore presented two size-matched larvae simultaneously to each set of ants, with one larva inside a refuge and the other on an unfolded leaf. I presented nine pairs in this way. Additional

tests included introducing larger larvae from a captive colony to test ant response to larval size, and leaving larvae in refuges in the ant jars for a full week.

Exposures to spiders were all made in small jars, by presenting larvae first in leaf refuges, usually for three hours; and then presenting the same larvae on unfolded leaves. This alternating sequence was repeated two to three times for some sets of larvae, to minimize the effects of order of presentation on spider behavior. I collected spiders from goldenrods and asters growing in the forest and placed them individually in the jars 1–2 days before adding a caterpillar. For spring trials I used spiders of a single, extremely common species, the theridiid *Theridion redimitum* (L.) Although these spiders are sedentary webspinners and seemingly unlikely to encounter equally sedentary larvae in leaf folds, I saw *Dichomeris* corpses with such spiders in the forest and concluded that webspinners were a significant threat, especially given their high numbers on the plants (Loeffler 1992). Morris (1972) also documented webspinners preying extensively on caterpillars. For fall trials I used the salticid *Metaphidippus protervus* (Walckenaer) (six individuals used), and the webspinning araneid, *Cyclosa conica* (Pallas) (12 individuals used), which were the two species of spiders most common on forest goldenrods and asters at that time. The lengths of exposures are indicated in Figs. 1 and 2. To factor out effects of a seasonal increase in spider size on capture success of the two species of caterpillars in the spring trials, I used not only field-collected larvae of both species but also *D. leuconotella* larvae from a captive colony that were phenologically synchronized with the later-developing *D. bilobella* and could be tested simultaneously with them. I compared survival rates of these three groups using a G-test with Williams' correction (Sokal & Rohlf 1981).

"Knockdown" trials. To determine whether larvae in refuges are better able to maintain contact with the plant should the plant be knocked to the ground by storms, falling branches, or passing mammals, I again let third to sixth instar larvae of *D. leuconotella* and *D. bilobella* build refuges on stem tops of the three types of goldenrods used for predator trials. Sample sizes for the different age classes of each species ranged from 15 to 38 larvae depending on supply and are indicated in Fig. 3. After refuges were completed, I overturned each stem with its larva onto a piece of paper, letting it fall by the weight of the water vial so that the force of the fall was consistent among stems. I recorded whether larvae maintained their position on the plants or fell onto the paper. Each trial was repeated with the caterpillar sitting outside its refuge, on the upper and then the lower side of the leaf or vice versa, and then once more with the caterpillar inside its refuge.

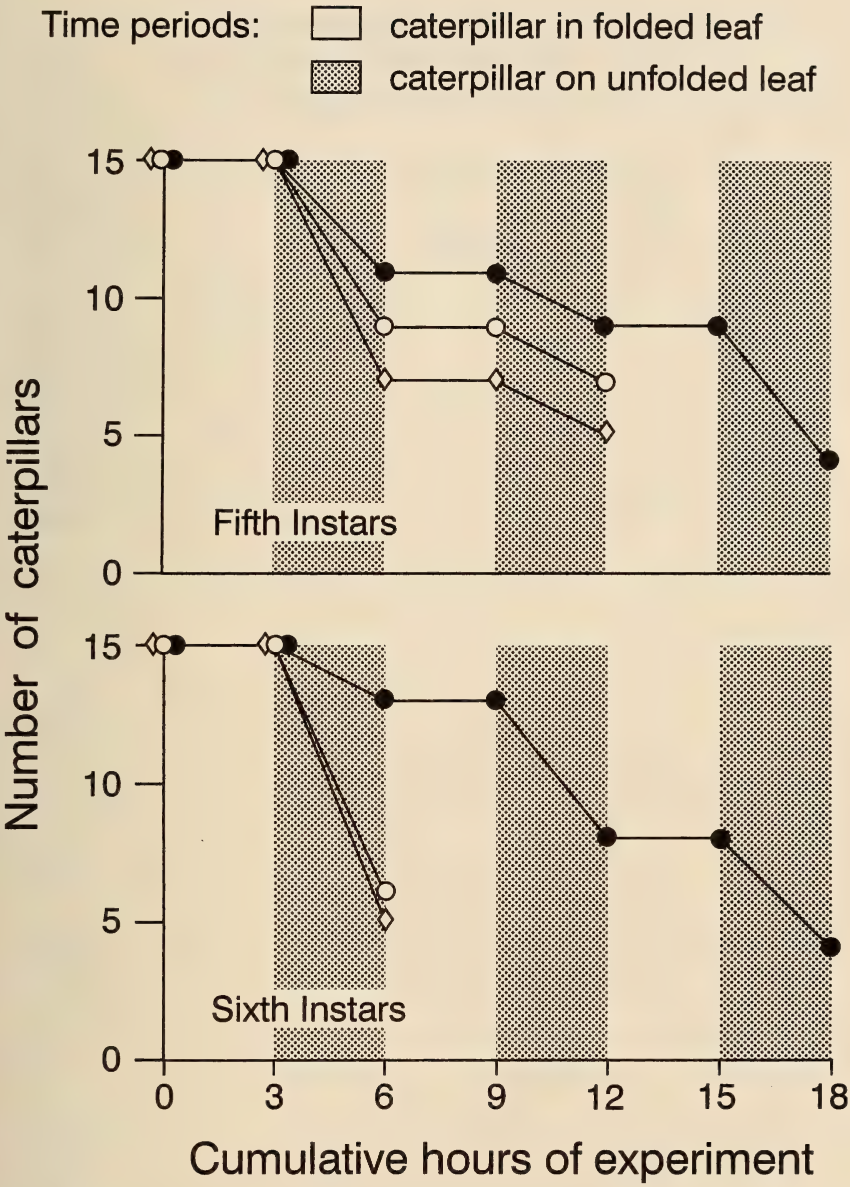

FIG. 1. Results of exposures of *Dichomeris leuconotella* and *D. bilobella* fifth and sixth instar larvae to spiders. Filled circles: field collected *D. leuconotella*, late May to early June 1988. Open circles: captive colony of *D. leuconotella*, early June to early July 1987. Open diamonds: captive colony of *D. bilobella*, early June to early July 1987.

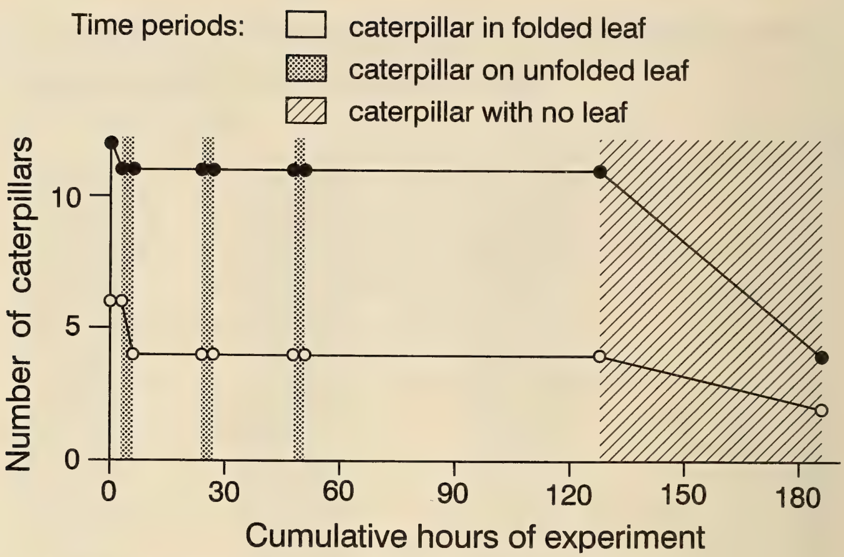

FIG. 2. Results of exposures of *Dichomeris leuconotella* third and fourth instar larvae to spiders in fall, 1987. Filled circles, exposed to araneid; open circles, exposed to salticid.

RESULTS

Predator Encounters

Ants and spring-feeding larvae. Results for the three goldenrod types were similar and will be discussed collectively. In general, *D. leuconotella* and *D. bilobella* caterpillars in leaf folds were safe from ant attack. *Formica* individuals crawled freely over the cut stem tops placed on their mounds in late spring. In each of the more than 360 "encounters" between ants and leaves bearing leaf folds with caterpillars, an ant spent from less than one second to more than a minute on the leaf, passing across or along the length of either surface. On 16 occasions, ants bit at the fold, but there was no indication of awareness of the larva inside and on five occasions ants bit more extensively or exclusively on the unrolled portion of the leaf. Such biting might be a means of obtaining water. Ants also bit frequently at other leaves, the stem, and the terminal bud.

Most of the folds, even those of final instars, appeared to be too narrow for ants to enter. Only three times did ants investigate the entrances of folds, and in the only case in which the ant actually entered the part of the fold occupied by the larva (a final instar *D. bilobella*), it became stuck and struggled for 4 minutes 36 seconds before managing to back out.

Most larvae did not react to ants simply moving over the fold. Reactions of larvae to ants biting or exploring the entrance to the fold in-

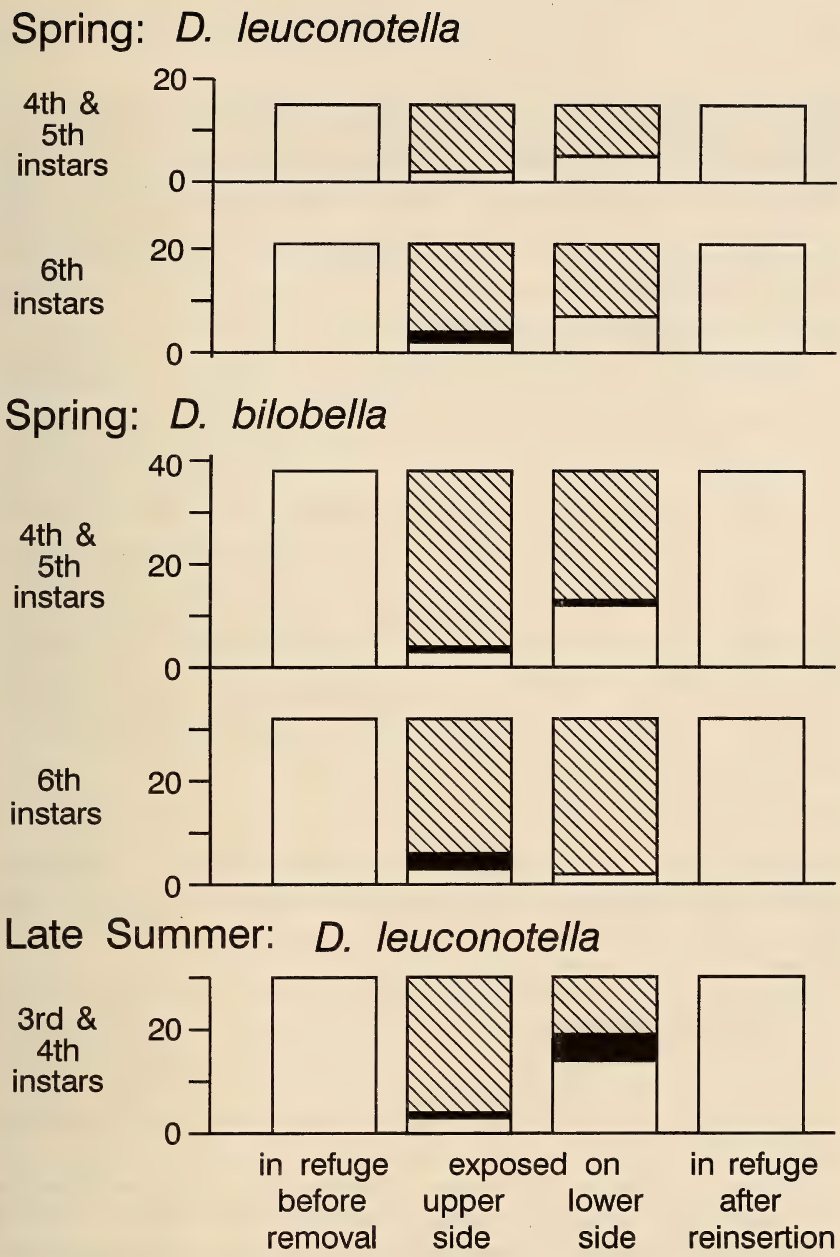

FIG. 3. Results of "knockdown" trials with *Dichomeris leuconotella* and *D. bilobella* fourth to sixth instar larvae in spring, and with *D. leuconotella* third and fourth instar larvae in late summer. Open bars are numbers of larvae that were not dislodged from their position in a refuge or on a leaf when their ramet top was overturned. Hatched bars are number of larvae dislodged from the ramet as it fell; solid bars are number of larvae that were dislodged from the leaf but landed on another portion of the ramet as it fell. The order of four trials was left to right as shown for half of the larvae; for the other half, the third trial (larva exposed on lower leaf surface) was run before the second.

cluded: 1) repeated jerking of the head fore and aft within the fold; 2) partial emergence from the end of the fold opposite the ant, sometimes accompanied by head jabbing and generally followed by quick retreat back into the fold; and 3) in two cases, complete emergence and rapid crawling from the leaf. The only caterpillar captured by ants during such maneuvers was one of the two larvae that emerged completely, the final instar *D. bilobella* in whose fold an ant became stuck. A second ant siezed the caterpillar as it emerged from the other end of the fold.

When the surviving 59 larvae were presented on ramet tops without leaf folds (as part of an alternating sequence of larva within fold, same larva outside fold, next larva within fold, etc.), 58 of the larvae were killed or forced to drop from the ramet after a total of 137 encounters. Thus, 79 encounters were "survived on the plant" and 58 involved the caterpillar being killed or losing contact with the plant (Table 1). Caterpillars without folds either sat still or slowly crawled over the leaves and stem of the plant top. Seven larvae began to fold leaves, and occasionally a larva made sufficient progress that I had to reopen the leaf. Ants frequently crawled on leaves bearing larvae without showing reaction to them, even from distances of <10 mm. But at other times ants ran directly to the larvae and attempted to bite them with their mandibles. The larvae reacted with violent wriggling, which, if initiated before an ant had its grip, propelled them to another leaf or off the plant. Sixth instars were more successful at escaping than fifth instars: ants succeeded in capturing 15 of 30 fifth instars on the plants compared to only two of 29 sixth instars (G-test for caterpillar species pooled: $G=14.62$, $df=1$, $p<0.001$; Table 1). An ant biting a caterpillar was usually joined by two or three others that helped subdue the larva and drag it off the plant and down a hole into the mound.

Wriggling was ineffective as a defense on the ground. Of 41 larvae dropping from the ramets (Table 1), ants attacked 22 and killed all of them. This attack rate is of course much higher than caterpillars would encounter in natural vegetation at lower ant densities, and these experiments do not indicate at what rate larvae dropping from a host plant would survive to locate and ascend another.

Only one caterpillar, a sixth instar *D. leuconotella*, remained alive and on the host plant ramet after six encounters with ants. This larva was one of three which sometimes responded to ant approaches by dropping off the leaf and dangling from a silk thread (the other two were fifth instar *D. bilobella*). Such a strategy was successful on four of five occasions, but one *D. bilobella* larva was forced to drop from the thread when the ant plunged after it.

Ants and fall-feeding larvae. Results of exposures of third and fourth instar *D. leuconotella* larvae to ants in September and early Octo-

TABLE 1. Results of exposures of 59 *Dichomeris leuconotella* and *D. bilobella* fifth and sixth instar larvae without leaf folds to ants. An "encounter" is defined as an occurrence of an ant on the same leaf as the larva. Each larva survived 0-6 encounters, for a collective total of 79 (top half of table, total numbers followed by breakdown); the 58 final encounters are indicated in the lower half of the table. In bottom half or table, in all cases, the ant approached within 1 mm.

	Number of encounters			
	D. leuconotella		D. bilobella	
	5th instars	6th instars	5th instars	6th instars
Caterpillar survives on plant:	18	21	23	17
Caterpillar reacts little, ant does not attack				
ant on opposite side of leaf	2	6	6	6
ant on same side, >10 mm from larva	11	9	10	7
ant within 1–10 mm of larva	2	2	1	3
ant within 1 mm or contacting larva	2	2	3	0
Caterpillar drops elsewhere on plant[1]	1	2	3	1
Caterpillar killed or drops from plant:	15	14[2]	15	14[3]
Caterpillar drops from plant,				
initially unpursued, wanders away	8	14	5	11
pursued by same ant, captured off plant	1	0	1	1
Caterpillar siezed by ants on plant	6	0	9	2

[1] After ant approached within 1 mm of caterpillar
[2] One of 15 caterpillars survived the requisite six encounters on the plant
[3] One of 15 caterpillars was killed earlier, when presented to ants inside its leaf fold

ber differed in that both caterpillars and ants showed less response to each other. Refuges of these smaller larvae were either folds or creases bridged by web. Ants several times touched or ran directly over exposed larvae, but in only one case did an ant attempt to bite a larva, and when the caterpillar wriggled out of reach, the ant turned away. Caterpillars generally remained still or edged forward slightly when touched by ants. Only once a caterpillar jumped off the leaf and dangled by a silk thread, hauling itself back onto the leaf after the ant had gone.

However, over a longer time span, exposed larvae were vulnerable. Two larvae that survived six encounters outside refuges were killed subsequently before they had time to construct refuges. In nine trials, I presented size-matched pairs of third and fourth instars to the ants, one in a refuge and the other exposed. The larvae in refuges survived, but seven of the nine exposed larvae were killed, all within approximately 1 h. This difference in survival was highly significant (G-test using Williams' correction, $G=10.59$, $df=1$, $p<0.005$).

Much of the ants' slowness of response appeared to be related to the caterpillars' small size. To test whether the ants would respond to large larvae as they had in spring, I presented one fifth and one sixth instar

D. leuconotella from a captive colony to ants in the field. Both were attacked and killed within five minutes. I also placed one fifth instar and two sixth instar *D. leuconotella* larvae in the same jars in which three third instars had just survived six encounters exposed on leaves. The three large larvae were attacked and killed within 13 min.

In a final series of tests, I left six third or fourth instar larvae in their refuges with the ants, and with additional goldenrod leaves and flowers, for a week. The ants remained healthy feeding on the flowers. All of the larvae survived except one killed toward the end of the week after its leaf turned wholly brown. Leaf senescence often correlates with a larva leaving its refuge (Loeffler, unpubl. data), although I did not determine if in this case the larva left its refuge before it was killed. At the end of the week I removed the remaining five larvae from their refuges and returned them to the jars. Three promptly hid themselves among flowers and two spun normal refuges on leaves. On the following (eighth) day I took the larvae out of their refuges again and removed all flowers from the jars, leaving only leaves. All five larvae were this time killed within 40 min. These results should be interpreted with some caution—they might indicate that ants were more likely to kill when flowers were absent, or that ants were more likely to kill on the eighth day than on the seventh. I consider the former more likely, because the ants fed on the flowers throughout the experiment and killed all five larvae promptly after the flowers were removed. The clear result, however, is that larvae were not killed until after they were taken out of their refuges.

Spiders and spring-feeding larvae. In spring trials, leaf folds of all three goldenrod types protected late instar caterpillars of the two species from attack by individuals of *Theridion redimitum* (Fig. 1). Spiders did not investigate the leaf folds, but sat unmoving in a sparse array of threads as they had in the field when collected. Many larvae emerged partway from their refuges at least once during a three hour exposure, and either fed for several minutes or simply defecated and returned to the refuge. None were caught on these occasions. When I subsequently placed the caterpillars into the same jars without refuges, many of them crawled about extensively. Such movement is not unnatural—after abandoning a refuge in the field, *Dichomeris* larvae often move past several leaf nodes on the stem and explore one to several leaf blades before settling on a fresh leaf and spinning a new fold (Loeffler 1992, 1993, 1994). The spiders often followed the moving larvae and attempted to bite them. The larvae wriggled on contact by the spiders, but some of those which momentarily escaped by this maneuver became tangled in the spiders' sparse webbing. Within an hour, most surviving larvae had ceased wandering and had settled down to fold new refuges. As indicated in Fig. 1, survivors in some groups of larvae were subjected to a

second or even a third round of presentations to the same spiders, first in a refuge for three hours, and then without a refuge. Combining these rounds, the total number of presentations of the 90 larvae first with and then without refuges was 147. The 147 presentations without refuges broke down as follows: on 76 occasions (52%), the larvae survived long enough to initiate a new fold and then survived the remainder of the three-hour test period. On 57 occasions (39%), larvae were killed before initiating a new leaf fold, almost always within an hour of being placed with the spider. On two occasions (1.4%), larvae were killed after initiating leaf refuges. Both cases involved captive colony final instar *D. leuconotella*. Both refuges were still partly open when the spider killed the larva; one was a fold with a 5 mm gap between sides, while the other consisted of a sparsely bound "sandwich" between leaf tips. On 12 occasions (8%), involving both species and both age groups, caterpillars survived a three hour exposure without constructing a refuge. Seven of these larvae and one of the 12 spiders were close to molting, which would account for less active behavior in those individuals.

Field-collected *D. leuconotella* had significantly higher survival rates (80% for age groups pooled in the first three-hour exposure without refuges) than either captive D. *leuconotella* (50%, $G=5.91$, $df=1$, $p<0.025$) or field-collected D. *bilobella* (40%, $G=10.09$, $df=1$, $p<0.005$). These results may reflect the fact that trials with field-collected *D. leuconotella* larvae took place earlier in the season when the spiders were smaller.

Spiders and fall-feeding larvae. Attack rates by the salticid, *Metaphidippus protervus*, and the araneid, *Cyclosa conica*, on third and fourth instar larvae of *D. leuconotella* in late summer were extremely low. The salticids rested on the jar either exposed or under a silk platform, and the araneids perched in sparse cobwebs. The caterpillars likewise moved little, spending their time resting, feeding, or applying silk to the leaves. In a long sequence of altemating exposures with and without refuges, only one larva with a refuge was killed, possibly while out feeding (Fig. 2). This larva was one of 12 exposed to araneids. The remaining larvae survived until the final exposure period, when not only refuges but all leaves were removed from the jars, and seven of the 11 (64%) were killed (Fig. 2). Among the six larvae exposed to salticids, two were killed during the first exposure without refuges, and two more were killed during the final exposure period without leaves. At each of several checks during this final exposure, usually about half of the formerly sedentary larvae were crawling on the jar and the other half were stationary. Both this increased movement and the greater exposure of the caterpillars in the empty jars may have prompted the increased attack rates. Increased hunger of the spiders with the passage of time may

also have contributed to the high attack rate, but had increased hunger been the sole factor involved, one might have expected at least some kills during the lengthy (77 h) period immediately preceding the removal of leaves from the jars (Fig. 2).

"Knockdown" Trials

None of the 106 caterpillars in these trials lost position within a refuge when the ramet tops fell over (Fig. 3). When the caterpillars lacked refuges, the frequency of dislodgment from an upper leaf surface ranged from 81 to 89% in the different age groups and species, while frequency of dislodgment from a lower leaf surface ranged from 53 to 94%. Each of these frequencies differed highly significantly from the zero rate of dislodgement of larvae within refuges ($p<0.001$ by G-tests for each position of larvae without refuges [upper or lower leaf surface] in each age group of each species). Larvae approaching molts could not maintain a grip on either surface and often fell off even before the sprigs were overturned, thereby demonstrating the necessity of a refuge at such times. Two groups were significantly less often dislodged from the lower leaf surface than from the upper surface: third and fourth instar D. *leuconotella* ($G=13.55$, $df=1$, $p<0.001$) and fifth instar D. *bilobella* ($G=6.20$, $df=1$, $p<0.025$).

Discussion

Leaf shelters have a wide variety of potential benefits in addition to protection from predation and dislodgment, such as maintaining a favorable microclimate (Wellington 1950, Henson 1958a, Henson 1958b, Willmer 1980, Hunter & Willmer 1989) and improving the chemical and nutritional suitability of leaf tissue within the shelter (Berenbaum 1978, Sandberg & Berenbaum 1989, Sagers 1992). These functions presumably vary in relative importance among caterpillar species; in some cases, certain effects of leaf shelters may be negative. An obvious example would be the use of leaf folds as a cue by visual predators such as birds which are capable of opening folds.

The ants and spiders tested in this study did not use folds as a cue and could not penetrate them to reach the *Dichomeris* larvae. Folds were effective protection whether they were tight or loose, and whether the leaf was thick or thin, hairy or smooth. The only capture of a larva in a fold resulted from an apparently inadvertent joint effort by two ants. As observed in this study, such instances are probably rare even where ants are concentrated near their nests, or are tending homopterans or lycaenid caterpillars.

Smaller spiders, ants, and other predaceous arthropods occur locally that could fit into late instar *Dichomeris* folds, but I have found little ev-

idence during extensive fieldwork that such small predators harm *Dichomeris* larvae.

Predaceous hemipterans may be capable of perceiving the larvae within leaf folds. I have watched a reduviid and a pentatomid waiting beside the entrances to leaf folds; indeed, the reduviid spent two days sitting astride the leaf fold before moving away without capturing the larva. But of predatory wasps and birds, which are potentially able both to associate folds with prey and to enter or open them (Steiner 1984, Damman 1987, Heinrich & Collins 1983), I have neither witnessed nor seen convincing signs of their attack on leaf folds over several field seasons in which I examined many hundreds of folds. Such predators might have much greater impact on tree- or shrub-feeding leaf folders (Heinrich 1979, Holmes et al. 1979).

Danthanarayana (1983) reported that earwigs commonly entered leaf rolls of the light brown apple moth and were important predators of that species. Earwigs were rarely seen on goldenrods in the areas that I worked (Loeffler 1992, 1993, and pers. obs.) and would be unlikely to fit into any but the largest *D. leuconotella* folds.

While leaf folds and webs are generally protective, the sedentariness associated with the leaf-folding habit may also be associated with lower probability of predator attack, inasmuch as it lowers the probability of encounter with sit-and-wait predators such as webspinning spiders. Young leaf folders remain for many days or weeks on a single leaf, and even large *Dichomeris* larvae, which change refuges every few days, move up or down a stem no more than a few nodes when changing refuges. In contrast, exposed feeders on goldenrods move frequently enough that they are rarely encountered near more than a day's worth of feeding damage (pers. obs.). Many exposed feeders, including some on nonwoody plants, are known for their long distance movements, which can average over a meter in a single night (e.g., Hansen et al. 1982). A factor of importance, however, is that many exposed feeders have evolved cryptic styles and timing of movement (Heinrich 1979, Stamp 1984a, Stamp & Bowers 1988, 1992, 1993), whereas *Dichomeris* larvae will move about seemingly indiscriminately at any time of day when feeding or changing refuges (Loeffler 1994, pers. obs.). Thus, although leaf folders are relatively well protected inside their refuges and less disposed to move, when they do move between refuges they may be more vulnerable than larvae of the average exposed-feeding species.

Dichomeris larvae do have two pronounced behaviors that help them escape when outside their folds: wriggling and dropping from the plant, and dropping on a silk thread without losing contact with the host. Both of these escape behaviors are also seen in exposed-feeding species (Allen et al. 1970, Stamp 1984b, 1986). In *Dichomeris* larvae, wriggling

is more effective as an escape mode in final instars than in younger larvae. Reavey (1993) and Stamp (1993) cite other instances in which older instars are less easily killed than younger instars.

Whether or not *Dichomeris* leaf folds also protect against parasitoids was not addressed in the present study, but it seems unlikely. Hawkins and Lawton (1987) found that "semi-concealed" insect herbivores such as leaf folders have relatively large numbers of parasitoid species, and indeed *Dichomeris* larvae have a large parasitoid assemblage (Loeffler 1994) which unlike the predators on goldenrods have apparently evolved mechanisms of dealing with leaf folds and which may indeed use the folds as cues.

The leaf fold also functions to keep *Dichomeris* caterpillars from losing contact with the host plant. The knockdown trials indicated that larvae in leaf folds could maintain their position even during violent movements of the host plant, as during wind storms or passage of a large animal. This function may be particularly important for molting larvae, which do not grip the leaf well. In other experiments (Loeffler 1996), early instars often wandered or fell from plants during refuge changes even though the plants were not disturbed at all. These results of course do not imply that leaf folding is the only or even the best way of maintaining contact with a host plant. Larvae of families such as the Geometridae and Noctuidae that typically feed exposed have a linear arrangement of crochets on their prolegs that enable them to maintain a more solid grip on the plant than can a gelechiid, whose circular arrangement of crochets is adapted for gripping a mat of silk within a refuge (J. G. Franclemont, pers. comm.). Thus, as with predation, dislodgment may be a negligible risk for *Dichomeris* larvae within their refuges but when changing refuges they may be more vulnerable than the average exposed feeder.

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GENERAL NOTES

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LIFE HISTORIES OF THREE *TAENARIS* SPECIES (NYMPHALIDAE: AMATHUSIINAE) IN PAPUA NEW GUINEA

Additional key words: *Musa*, *Pandanus*, mimicry, parasitism, natural enemies.

Papua New Guinea, Irian Jaya and their satellite islands support a number of species in the butterfly genus *Taenaris* Fruhstorfer. *Taenaris artemis* Vollenhoven, *T. catops* Westwood and *T. myops* Felder closely resemble each other, occur sympatrically and are members of a Müllerian mimetic complex (along with *Hyantis hodeva* Hewitson; Vane-Wright 1971, Parsons 1991). Adults of these *Taenaris* species have striking, possibly aposematic color patterns, with large bright yellow or orange eye-spots on a dark or white background. Although the recorded larval foodplants of these species are not known to be toxic, adult *T. catops* appear to indulge in pharmacophagy of cycad juice (Parsons 1984, Merrett 1993), which contains a toxic MAM-glycoside (cycasin) possibly making them unpalatable to predators (analysis of dried specimens of *Taenaris* has revealed the presence of cycasin in *T. catops* but not in *T. myops*; Nash et al. 1991).

The purpose of this paper is to provide new life history data for the subspecies *Taenaris artemis staudingeri* Honrath, *T. catops westwoodi* Staudinger and *T. myops kirschi* Staudinger. *Taenaris artemis staudingeri* and *T. myops kirschi* occur in eastern Papua New Guinea, and *T. catops westwoodi* occurs from Geelvink Bay in Irian Jaya to the Herzog and Rawlinson Mountains in Papua New Guinea (D'Abrera 1977).

Searches for larvae and ovipositing females of *Taenaris* were made at the National Botanic Gardens in Lae, Morobe Province; at the Papua New Guinea University of Technology; and villages in the Boana District, Morobe Province. Wild butterflies were netted in flight, or trapped at fermenting banana bait. Females were sleeved in net bags over cut leaves or whole plants in pots to induce oviposition. Voucher specimens of *Taenaris* larvae and pupae have been deposited in the Natural History Museum, London.

Taenaris artemis staudingeri

Table 1; specimen voucher numbers BMNH ES 3233-3237.

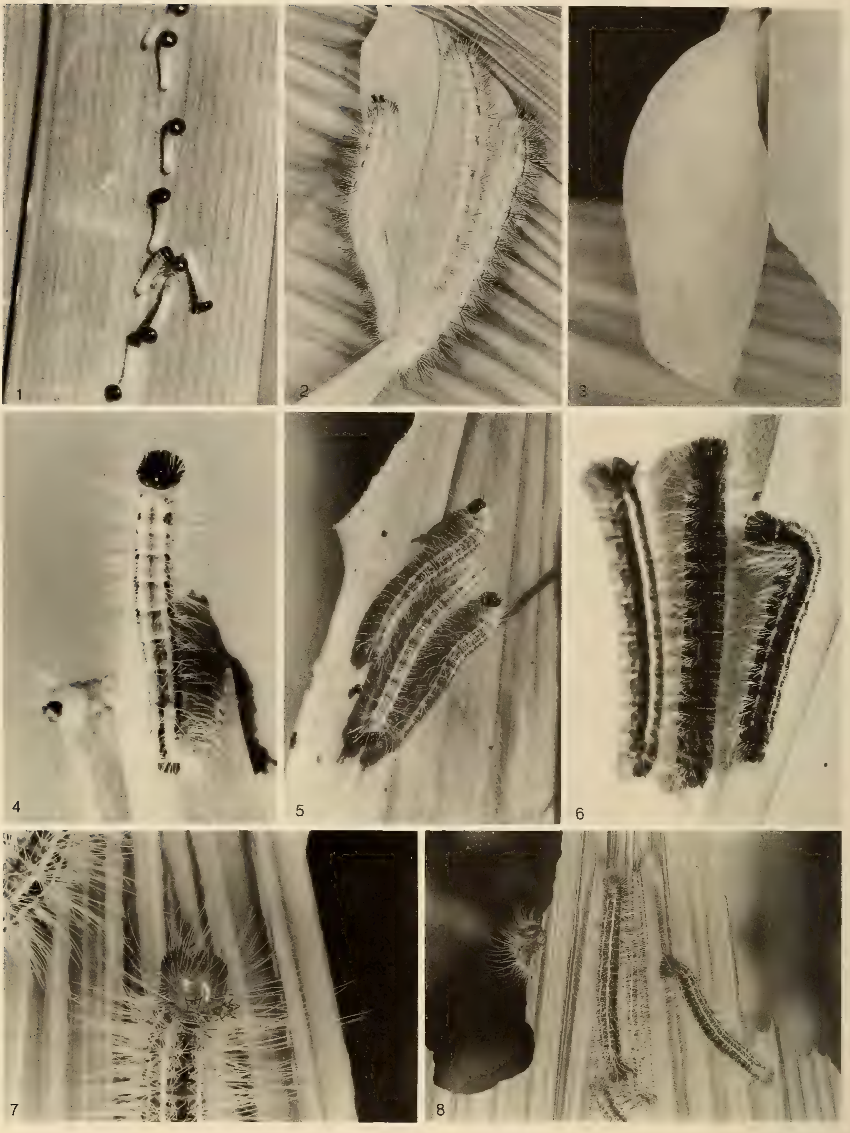
Egg (n=271). Roughly spherical, greenish, becoming pinkish; laid in batches on underside of *Pandanus* spp. fronds; diameter circa 1.5 mm.

First instar (n=264). Head shiny dark brown with white 2 mm hairs (Fig. 1); dorsolaterally, prothorax bears two blackish tubercles; meso- and metathorax bear two orange tubercles; anal segment bears dark dorsal plate; body pale orange becoming greenish with age (prothorax and posterior abdominal segments developing brighter orange), covered with white hairs; mid-dorsal line slightly darker orange; spiracles orange; head capsule width slightly less than 1 mm; larva grows to 4-8 mm in length.

Second instar (n=136). Head brown or black with two dorsolateral, forward-pointing brown horns bearing six translucent spines each, central longest; body light green, orange tint to dorsal thorax and segments A10–A11 (Parsons [1984] recorded the larvae of *T. artemis jamesi* Butler as predominantly yellow marked with black); prothorax bears two dorsolateral dark green welts; mesothorax and metathorax bear pairs of dorsolateral, orange tubercles; tubercles decrease in size caudally; head and body clothed with short and long white hairs, 3 mm on thorax; dark green mid-dorsal line; lateral coloration green with broken, creamy white line joining brown spiracles; head capsule width 1.5 mm; larva grows to 10 mm in length.

Third instar (n=120). Spines on horns from short pedicels marked with brown rings; dorsolateral tubercles of prothorax less pronounced; intersegmental membranes and underside lighter green than rest of body; segments A8-A10 brighter orange than in second instar; dorsal line outlined with darker green; creamy white dorsolateral lines; head capsule width 2 mm; body hairs 3 mm; larva grows to 20 mm in length.

Fourth instar (n=173). Dorsolateral, orange tubercles on each body segment become



FIGS. 1–8. Immature stages of *Taenaris* species. 1-3: *Taenaris artemis staudingeri* Honrath. **1**, first instar larvae; **2**, fifth instar larvae; **3**, pupa. 4–6: *Taenaris catops westwoodi* Staudinger. **4**, fourth instar larva; **5** and **6**, fifth instar larvae. 7–8: *Taenaris myops wahnesi* Heller. **7**, fifth instar larva (showing horns); **8**, fifth instar larvae.

TABLE 1. Duration in days of immatures of *Taenaris artemis staudingeri* reared at circa 27°C: means, ranges and sample sizes (n). Rearing batches: 1, wild-collected fourth instar larvae, 12 November 1986; 2, wild-collected second instar larvae, 4 February 1987; 3, from eggs laid by female, September 1987; 4, from eggs laid by female, May 1988; 5, from eggs laid by female, August 1988; 6, from eggs laid by female, September 1988.

Brood		Life Stage								
		Egg	L1	L2	L3	L4	L5	L6	Pupa	Total
1	mean	—	—	—	—	—	10	—	10.5	—
	range	—	—	—	—	—	8–11	—	9–12	—
	n	—	—	—	—	—	33	—	25	—
2	mean	—	—	—	6	6	12	14.5	11	—
	range	—	—	—	6	6	7–16	14–15	9–14	—
	n	—	—	—	46	43	38	4	28	—
3	mean	11	7	12	7	5	5.5	—	11	40
	range	5–14	7	7–12	7	5	4–9	—	10–11	39–42
	n	88	30	24	17	14	4	—	3	3
4	mean	9	8	8	5	—	—	—	—	—
	range	9	8	8	5	—	—	—	—	—
	n	17	17	17	17	—	—	—	—	—
5	mean	11.5	—	—	—	—	—	—	10.5	76
	range	10–12	—	—	—	—	—	—	9–12	67–81
	n	51	—	—	—	—	—	—	7	15
6	mean	12	5	4	6.5	—	—	—	12	53
	range	12	5	3–4	5–7	—	—	—	10–14	48–58
	n	74	44	49	40	—	—	—	7	9

continuous welts, with white hairs (5 mm) and shorter darker hairs, surrounded by orange cuticle; segments A8-A10 entirely orange; spiracles orange, outlined black, ringed by orange; above spiracles are two lateral, creamy white lines; head capsule width 3 mm; larva grows to 28 mm in length.

Fifth instar (n=75). Head capsule shiny, light brown, mottled black (Fig. 2); mean width 4.6 ± 0.2 mm (n=23); horns and lateral ocelli black; up to two extra spines may be present on horns; mouthparts strongly sclerotized; orange dorsal prominences on each segment continue laterally to spiracles, ringed by greenish orange cuticle; each thoracic segment has dorsolateral prominence; each abdominal segment has two dorsolateral welts, two creamy white, transverse lines between, and one anterior transverse line; dorsally grey hairs tipped with black, 6 mm, on thorax; lateral hairs shorter, denser; segments A5–A10 flushed orange; first six intersegmental membranes creamy yellow; dorsal line alternately black, from anterior of segment through orange prominences, and lighter green, from prominences to posterior; dorsolateral and super-spiracular lines creamy yellow; larva grows to 30-56 mm in length.

Sixth instar (n=6). Presumed supernumerary (two larvae died and four emerged as females); head capsule width 5 mm, shiny light brown with black horns, ocelli and mouthparts; coloration as in fifth instar; thoracic hairs up to 6 mm; larva grows to 41 mm in length.

Pupa (n=70). Light green with two pale yellowish points on head (Fig. 3); dorsolaterally, prothorax has two yellow spots set in yellowish green patch; more dorsally, mesothorax bears two shiny grey spots; wing cases translucent; abdomen paler green; cremaster and its supports black with dark green ovoid between roots of supports; length 30 mm, width 10 mm; similar in appearance to pupae of *T. myops* and *T. catops*.

Foodplants and biological notes. In 1987 and 1988, six wild-collected females were sleeved in net bags over cut leaves of *Pandanus* sp. or whole plants of *Pandanus odorus* Ridl. (Pandanaceae). These six females laid 230 eggs in four batches (Table 1). A seventh female was sleeved over both *P. odorus* and *Curculigo erecta* Lang (Amaryllidaceae), and she laid 41 eggs on *C. erecta*; 34 larvae hatched and fed but died during the next moult. Two wild larval batches were collected from *Pandanus* in 1986 and 1987 (Table 1). In a feeding experiment, six fifth instar larvae from the 1986 batch were offered *Cocos nucifera* L. (Palmae) leaves, upon which they successfully completed development.

Larvae fed on the undersides of tough, spiny fronds of *Pandanus*, consuming the frond from the tip down to the base before moving on. Larvae were gregarious during instars one through four, and tended to feed and molt synchronously. Fifth instar larvae became more solitary. Although the gregarious habit may be linked to unpalatability in *Taenaris artemis* (Vane-Wright 1971), as is certainly the case in *T. onolaus* (Parsons 1984), leaves of *Pandanus* are not known to be toxic, and the fruit of some *Pandanus* is prized as food in Papua New Guinea (species eaten include *P. conoideus*, *P. jiulianetii* Mart. and *P. brosimos* Merr. & Perry; May 1984).

Parsons (1984) recorded the foodplant of *Taenaris artemis* as coconut, *Cocos nucifera*, and that of *T. artemis jamesi* from the Western Province of southern Papua New Guinea as *Pandanus* sp.

Over 50% of the wild-collected larvae from batch 1 were parasitised by *Apanteles* sp. (Hymenoptera: Braconidae). No larvae from batch 2 were parasitised. Two of nine pupae in batch 6 were attacked by *Brachymeria* sp. (Hymenoptera: Chalcididae), with 19 individuals emerging from one larva. Many of the larvae bred *ex ovis* were killed by immature sucking bugs, *Montrouzierellus melacanthus* (Boisduval) (Heteroptera: Pentatomidae: Asopinae). Larvae of *T. artemis staudingeri* may be protected to some extent from parasites by dense pubescence. When provoked, fifth instar larvae tuck their heads under the prothorax and present their horns.

Taenaris catops westwoodi

Table 2; specimen voucher numbers BMNH 3229-3232.

Egg (n=94). Greenish, becoming greyish from the center before hatching; diameter circa 1.5 mm; laid in batches.

First instar (n=69). Head capsule shiny dark brown to black; body whitish green, 3 mm white hairs on meso- and metathorax, slightly shorter on A5 and A6; head and body clothed with short white hairs arising from tubercles; anal segment has short black hairs; larva grows to 4-8 mm in length; head capsule width slightly less than 1 mm.

Second instar (n=39). Head bears two short black dorsolateral horns with seven spines each, and white hairs; body greenish with two dorsolateral creamy white lines, between lines two rows of dorsolateral tubercles bearing white hairs; sides of thorax and segments A1-A6 and prolegs greenish with black spiracles, connected by faint creamy line; Segments A7-A8 have orange patch around spiracles; segments A9–A10 flushed with orange, including anal prolegs; body clothed in white hairs, longest (up to 3 mm) on prothoracic and anal segments; larva grows to 5–11 mm in length; head capsule width just over 1 mm.

Third instar (n=27). Prothorax to A8 dark or greyish green; orange patches around each spiracle; from segments A7–A10 arise two broken black lines either side of midline, terminating in black anal plate bearing two short brown papillae with short brown hairs; on segments A7-A8 black marks between dorsolateral line and spiracles; apart from these black marks, larva matches description by Parsons (1984); white hairs on thorax up to 4 mm; larva grows to 9-16 mm in length; head capsule width 1.5–2 mm.

Fourth instar (n=15). Eight with continuous black dorsal and dorsolateral stripes as in Parsons (1984), one with a broken black line (Fig. 4) and two with a dark green line; between dorsal and dorsolateral lines are green and then white lines; dark green to black

TABLE 2. Duration in days of immatures of *Taenaris catops westwoodi* reared at circa 27°C: means, ranges and sample sizes (n). Rearing batches: 1, from eggs laid by female, August 1987; 2, from eggs laid by female, September 1987; 3, from eggs laid by female, July 1988.

Brood		Life Stage Egg	L1	L2	L3	L4	L5	Pupa	Total
1	mean	8	—	—	—	—	—	—	—
	range	8	—	—	—	—	—	—	—
	n	14	—	—	—	—	—	—	—
2	mean	10	7	6	7	14	13	—	—
	range	10	7	6	5–12	13–14	13	—	—
	n	14	14	12	12	3	1	—	—
3	mean	10	11	9	—	—	10.5	13	85
	range	9–10	10–11	8–11	—	—	10–11	13	85
	n	38	26	15	—	—	2	1	1

dorsolateral lines extend to segment A8, where these terminate in orange patch around last spiracle; legs and prolegs flushed with orange; prothorax has dark brown collar; black anal plate surrounded by black hairs; 6–7 mm white hairs on thorax and segments A8-A9; larva grows to 15-35 mm in length; head capsule width 3 mm.

Fifth instar (n=7). Color variable (see Figs. 5–6), ranging from nearly black (as in Parsons 1984) through dark brown to greenish grey; brown specimens have yellowish brown dorsolateral lines, black larvae have faint white lines; black dorsal and dorsolateral lines complete; black spiracles ringed with orange patches, connected by light orange to creamy line, reduced to orange spots in black larvae; prolegs light orange or pink, with black basal spot in black specimens; extra spine may be present on horns; prothorax greyish without lines; larva grows to 25-37 mm in length; head capsule width 4–4.5 mm; 8 mm hairs on thorax and segments A8-A9.

Pupa (n=2). Light apple green with two short yellow horns on head; thorax slightly humped and 10 mm at widest; cremaster yellow basally and black apically; length circa 32 mm.

Foodplants and biological notes. Parsons (1984) listed *Cordyline terminalis* (Liliaceae) and *Phaius tancarvilleae* (Banks in L'Herit) Bl. (Orchidaceae) as larval foodplants of *Taenaris catops westwoodi*. D'Abrera (1977) listed *Caryota rumphiana* Mart. (Palmae), *Areca catechu* L. (Palmae), *Musa acuminata* Colla, and *M. balbisiana* Colla (Musaceae), and the Insect Farming and Trading Agency (Ipou, pers. comm.) added the ground orchid *Spathoglottis* (Orchidaceae).

In the present study, three batches of eggs were obtained by sleeving five females over potted *Caryota rumphiana* (Table 2). All the aforementioned foodplants were available for testing except the two recorded by Parsons. The larvae from batch 1 refused to eat any of the foods offered, and died. Larvae from batch 2 fed on *C. rumphiana*, but died before pupation. Three larvae from batch 3 (which was begun on *C. rumphiana*) switched to a neighboring *Pandanus* plant, and pupated on it. The later instar larvae reared in this study appeared sick, and this may have contributed to increased mortality and/or protracted larval periods.

Taenaris catops westwoodi is a potential economic pest of *A. catechu* (which is widely used as a mild stimulant in Papua New Guinea) and of *C. rumphiana* (which is used as an ornamental, a famine food and for making bows).

Taenaris myops wahnesi

Table 3; specimen voucher numbers BMNH (E) 1994-109, tube nos. 4007–4008.

Egg (n=105). Roughly spherical, pale green becoming pinkish red in 1–2 days; laid in batches on the underside of leaves.

First instar (n=105). Shiny, light brown head capusle, width slightly less than 1 mm, bearing short white hairs and two small bumps; greenish body 4 mm, bearing longer white hairs; posterior abdominal segments become pinkish or orange with age; two dark tubercles on orange prothorax, spiracles dark.

Second instar (n=85). Head bears two short horns, each with crown of five translucent spines surrounding central knob; body pinkish with two paler dorsolateral lines and two paler lateral lines, interrupted by pinkish patches around each spiracle; segments A8-A10 pinkish or yellowish orange; head capsule width just over 1 mm; body 7 mm in length, with 3 mm white hairs arising from dorsolateral tubercles on thorax.

Third instar (n=58). Head brownish orange with black spines and stemmata; horns darker brown; body orange to pinkish or wine red, darker from mesothorax to segment A7 (cf. Parsons' [1984] report of steady darkening in brownish black second to fourth instar *T. myops kirschi*); thoracic segments each bear transverse ridge dorsally; spiracles brown, ringed with black, surrounded by orange patch; posterior abdominal segments and underside orange; head capsule width 1.5 mm; hairs 7 mm; larva grows to 11-18 mm in length.

Fourth instar (n=46). Body brownish red from orange prothorax to segment A7; dark brown dorsal stripe, two white dorsolateral lines and two white lateral lines; body hairs 10 mm, arising from white tubercles; two white transverse lines on side of segment A9; underside reddish orange; head capsule width 2 mm; larva grows to 20–32 mm.

Fifth instar (n=14). Head reddish orange, body dark wine red (Figs. 7–8), contrasting with descriptions for *T. myops kirschi* Staudinger (dirty greyish yellow, Szent-Ivany & Barrett 1956; black and unlined, Parsons 1984); segments A6-A8 orange; body bears 9 mm white hairs and shorter black ones; mean head capsule width 4.4 ± 0.2 mm (n=14) across; larva grows to 25-45 mm in length.

Pupa (n=10). Light green, with two yellowish horns on head; external sex distinguishing marks brownish; cremaster yellowish green marked with black, 2.5 mm; two whitish wavy dorsolateral lines; length 26-29 mm, width 9-10 mm at first abdominal segment.

Foodplants and biological notes. Females of *Taenaris myops wahnesi* were confined on *Musa acuminata* Colla and *M. balbisiana* (Musaceae) (n=5), *Ptychosperma robusta* (Palmae) (n=3), and *Curculigo erecta* (n=1). The females confined on *P. robusta* and *C. erecta* oviposited readily, but no eggs were laid by the females confined on *Musa* (a foodplant reported by Szent-Ivany & Barrett 1956).

Three egg batches were obtained and rearded from these females (Table 3). Larvae from batch 2 refused to eat *Ptychosperma robusta* leaves. When they were offered cut leaves of banana, *Costus* sp. (Costaceae), *Cocos nucifera* and *Areca catechu* instead, they fed until the third instar on *Costus* sp. and then on banana leaves. Larvae from batch 3 fed successfully on *P. robusta*. Fifteen of these larvae were forced at the third instar onto *C. nucifera* (a foodplant recorded for *T. myops kirschi* [Anon 1969] and *T. myops* [Szent-Ivany, pers comm.]), *Areca catechu* and banana. Only four of the larvae held on banana survived to pupation. Larvae from batch 4 were fed solely on *C. erecta*, and only one adult was produced.

Five wild *Taenaris myops wahnesi* larvae were found on a hybrid *Ptychosperma robusta* in August 1986, and two others were found on cultivated banana in May 1987 (Table 3). Parsons (1984) collected larvae of *T. myops kirschi* on *Tapenochilus* sp. (Costaceae) in the Port Moresby District of southeastern Papua New Guinea, and the Insect Farming and Trading Agency (Ipou, pers. comm.) has recorded larvae of *T. myops wahnesi* feeding on *Costus* sp. near Bulolo, in northern Papua New Guinea. *Taenaris myops* is known as a pest of banana, *Musa acuminata* and *M. balbisiana* (Szent-Ivany & Barrett 1956), coconut, *Cocos nucifera* (Anon 1969 and Szent-Ivany, pers. comm.) and oil palm, *Elaeis guineensis* Jacq. (Palmae) (Prior, pers. comm.).

One pupa from a wild larva taken on *Ptychosperma* sp. yielded a tachinid parasite (Diptera). It is possible that the wine red larvae of *T. myops wahnesi* are aposematic, like

TABLE 3. Duration in days of immatures of *Taenaris myops wahnesi* reared at circa 27°C: means, ranges and sample sizes (n). Rearing batches: 1, wild-collected fourth instar larvae, August 1986; 2, from eggs laid by female, 2 October 1986; 3, from eggs laid by female, 9 October 1986; 4, from eggs laid by female, September 1988.

		Life Stage							
Brood		Egg	L1	L2	L3	L4	L5	Pupa	Total
1	mean	—	—	—	—	—	7	14	—
	range	—	—	—	—	—	7–11	14	—
	n	—	—	—	—	—	3	1	—
2	mean	11	5.4	7	4	5	14	12	64
	range	11	5–7	7–10	4	5	14	11–15	60–68
	n	27	27	9	5	4	1	2	2
3	mean	10	7	5	5	7	10	11.5	57
	range	10	7	5	5	8–13	9–11	10–13	55–59
	n	59	59	57	34	24	8	4	4
4	mean	11	6	6	6	6.5	14	13	65
	range	11	6	6	6–8	6–7	9–17	13	65
	n	19	19	19	19	18	3	2	1

the similarly colored larvae of the *Cycas*-feeding *Taenaris onolaus* and *T. butleri* Oberthur (Nash et al. 1992).

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CHARLES REMINGTON'S CONTRIBUTIONS TO THE SPECIES CONCEPT

Additional key words: speciation, hybridization, hybrid zones.

The following remarks were written with the encouragement of the Editor in order to supplement issue 49(4) of the *Journal*, which commemorated the career of Charles Remington. I first met Charles Remington in 1971 at the Pacific Slope meeting of our Society, at which he gave a talk on the special aspects of genetic divergence and speciation on islands. His presentation, as in his writing, was authoritative, detailed, liberally spiced with interesting non-lepidopteran examples, and delivered with conviction. Charles Remington has long held a special interest in speciation. No topic is more central to evolutionary theory, nor more controversial, and those with strong conviction soon themselves become controversial.

Remington was an early proponent and remains a strong advocate for the "Biological Species Concept" (BSC), wherein species are thought to arise by genetic divergence in isolated populations, and are defined by presumed (the usual case) or by demonstrated (less often) reproductive isolation from closely related taxa. Traits serving this isolation function are assumed to have evolved through, or were perfected by, selection favoring the reduction of wasteful interspecific hybridization. Early criticism of the BSC stressed the difficulty in demonstrating reproduction isolation, especially between allopatric populations of organisms not amenable to experimental hybridization. Indeed, the great majority of lepidopteran species and subspecies are based on comparisons of wing pattern and genitalia, not on demonstrated mating barriers or measured hybrid fitness. More recently, the "Recognition Concept" proposes that reproductive isolation is only an incidental byproduct of adaptations increasing reproductive success through the evolution of species-specific mate recognition systems. Hybrid zones would seem a likely setting to observe the perfection of incipient reproductive isolation, yet few convincing examples have been found among many detailed studies. The apparent long-term stability of hybrid zones conflicts with Remington's view that they should be ephemeral, quickly evolving toward either fusion or toward speciation and a cessation of hybridization (see Collins 1991 and Coyne 1994 for reviews of these controversies).

The divergence in allopatry tenet of the BSC has endured, partly because biogeographic patterns of variation support it, and also because population genetics theory shows that even low rates of gene flow can prevent divergence between adjacent populations. Remington's early papers cited intriguing patterns of phenotypic variation, and advocated the active pursuit of studies in geographic variation and speciation by lepidopterists (Remington 1951, 1958). The work of his graduate student Charles Oliver was a product of this period, in which Oliver hybridized intra- and interspecific populations to reveal geo-

graphic variation in genes controlling reproduction and development (Oliver 1972, 1978, 1979a, 1979b. 1980). These studies complemented allozyme surveys of variation in genes coding for protein synthesis, and showed that the genetic basis for hybrid incompatibility may first arise within a species as regional ecological adaptations. In spite of the fact that Lepidoptera are relatively easily collected and bred, few other studies of this type have been conducted.

Many natural hybrid zones are known in Lepidoptera, and Remington was among the first to recognize their importance as natural laboratories in which to study the genetics of speciation. His "suture zone" paper (Remington 1968a) is now considered a classic in which he provided examples among varied animal taxa of hybridization along well-defined zones. The geographic location of these zones, and concordant distribution among unrelated taxa, strongly support the model of secondary hybridization as a result of range expansion from Ice Age refugia.

Remington's unwavering support of the BSC may lie in the appeal of the explanatory power of the genetic mechanisms thought to promote the formation of species: genetic divergence in the absence of homogenizing gene flow; selection against wasteful hybridization upon secondary contact of such divergent populations; the origin of reproductive isolation; speciation accomplished. Remington has often referred to these processes as "sequelae," and his deterministic view of speciation is reflected in his title "Genetic differences in solutions to the crises of hybridization and competition in early sympatry" (Remington 1985). The current view of species, following two decades of applying molecular techniques of genetic analysis, reveals a pattern of uncoupled evolution among categories of traits. Premating isolation, postmating compatibility, morphological characters, and physiology may evolve at vastly different rates. Some very similar species can exist in sympatry (sibling species), and other distinctly different species may freely hybridize in the lab or along hybrid zones. Many animal species simply cannot be defined on the basis of effective reproductive isolation.

Remington has long advocated experimental hybridization as a means to understand speciation (Remington 1958). Ironically, in one of his few species descriptions, Remington (1968b) was unable to obtain critical test crosses between his *Papilio gothica* and *P. zelicaon*, and the former is now thought by some to be an example of seasonal polyphenism in the latter. Recent cladistic studies (e.g., in the frog genus *Rana*, Hillis 1988) have shown that measures of reproductive compatibility from experimental hybridization may not be concordant with phylogenetic relationships established on the basis of molecular and morphological traits. In these examples, those taxa that freely hybridize may not be as closely related as other pairs showing reproductive isolation. For this reason, and because hybridization can lead to reticulate (vs. branching) evolution, advocates of the phylogenetic species concept spurn experimental hybridization data in their analyses. Yet, as Remington has so forcefully stated, laboratory crosses are extremely useful in revealing differences among species for regulatory genes controlling reproduction and development (e.g., Collins 1984). The proper phylogenetic interpretation of hybrid data can be derived from independent cladistic studies using molecular and other character sets (Avise & Ball 1990). Unfortunately, with several notable exceptions (see Lorkovic 1985, Sperling 1987, Powell 1995, Scriber et al. 1996, Tuskes et al., 1996), too few multidisciplinary works have been done in Lepidoptera taxonomy. Let us hope that the new generation of workers, with their powerful molecular techniques, will read and be stimulated by Charles Remington's insightful writings.

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DONATION OF THE ATSUSHI KAWABE LEPIDOPTERA COLLECTION TO THE SMITHSONIAN INSTITUTION

Additional key words: *Archips*, Tortricidae, Japan, Taiwan, Thailand.

On 27 November 1993, Atsushi Kawabe, a leading authority on Japanese Tortricidae, passed away at the age of 57 in Tokyo, Japan. Mr. Kawabe was born on 10 January 1936 in Ishikawa Prefecture, and after 1955 he lived in Setagaya, Tokyo and Chiba Prefecture

where he was an inspiring teacher in biology at a private high school. Although probably considered an amateur by stricter standards, his research productivity in entomology exceeded that of many "professionals." Mr. Kawabe published approximately 200 scientific papers, most dealing with the moth family Tortricidae of Japan, Taiwan, and Thailand. Thirty three of these papers, including most of his later ones were written in English. The publications for which he will probably be best remembered are his "Revision of the genus *Archips* from Japan" (Tyo to Ga 16:13–40, 1965) and "Records and descriptions of the subfamily Olethreutinae from Thailand" (pp. 23–82 *in* S. Moriuti (ed.), Microlepidoptera of Thailand, No. 2, 1989).

It was Mr. Kawabe's wish and our hopes that his collection of Lepidoptera be donated to the Smithsonian Institution. Although more than 16 families of predominantly Japanese and Taiwanese moths are represented in this excellent collection, over 75% of the 22,038 specimens accessioned are members of the family Tortricidae—his taxonomic specialty. Of special importance are the holotypes of 95 species and subspecies described by Mr. Kawabe and a few coauthors.

The Smithsonian Institution wishes to thank Mrs. Sumiko Kawabe for seeing that her late husband's wishes concerning his collection were carried out, and to his close friend and colleague, Mr. Yasutoshi Shibata, for all his considerable efforts in arranging the shipment of this collection.

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Cover illustration: adult male of the lasiocampid moth, *Tolype velleda* Stoll, at rest on a fallen leaf in the artist's back yard. Original pen and ink drawing by John Himmelman, 67 Schnoor Road, Killingworth, Connecticut 06419, USA.

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POPULATION BIOLOGY OF *HETEROSAIS EDESSA* (NYMPHALIDAE) AND ITS ASSOCIATED ATLANTIC FOREST ITHOMIINAE COMMUNITY

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ABSTRACT. The early stages of *Heterosais edessa*, an advanced species of Ithomiinae (Nymphalidae) are described. Adult population size, sex ratio, longevity, food resources and movement are given for this species and compared with those of 17 other members of the local Ithomiinae community.

Additional key words: mark-recapture, Godyridini, *Cestrum*, Solanaceae, K-strategist.

Long term population studies may reveal important features of ecology and adaptation in tropical butterflies (Ehrlich 1984). DeVries (1994) emphasized the importance of such studies as a basis for understanding Neotropical butterfly communities, encouraging studies of life histories. The Ithomiinae, along with the Heliconiini, attracted the attention of early naturalists as central models of mimicry rings in the Neotropics (Bates 1862, Muller 1879), but there are few works concerning population ecology of ithomiine butterflies (Brown & Benson 1974, Drummond 1976, Haber 1978, Vasconcellos-Neto 1980, 1986, 1991, Young & Moffett 1979, Freitas 1993).

Heterosais edessa is a common ithomiine species found in humid primary and secondary forests, mostly in coastal southeastern Brazil, being rare on mountain slopes and nearly absent on the central plateau. Other closely related species or subspecies extend throughout the Amazon and as far northwest as Costa Rica. *Heterosais* is considered one of the most advanced genera within the Ithomiinae (Brown & Freitas 1994), and the study of ecological parameters in this genus may help in the understanding of the evolution of this subfamily.

This paper describes the juvenile biology of *H. edessa* and its adult population ecology in relation to other species of the associated ithomiine community.

STUDY SITE AND METHODS

Observations were made from July 1988 to July 1992, in the locality of "Morro do Japuí" (46°24'W 23°59'S), São Vicente, São Paulo, Brazil. The study area is covered by submontane rain forest (Ururahy et al 1987), with an annual rainfall near 2500 mm and an average annual temperature of 21°C (Setzer 1949, Prodesan 1969, Nimer 1972). A large part of the area is secondary forest, with a predominance of forest edge plants. A detailed map of the locality is given in Freitas (1993).

In order to study the life cycle of *H. edessa*, eggs and larvae were collected on individuals of the host plant species, *Cestrum laevigatum* Schldl. (Solanaceae), in the forest. Larvae were reared on leaves of this host in plastic boxes, cleaned daily. Egg size is presented as length and diameter, and the head capsule size of larvae as the distance between the most external ocelli (as in Freitas 1991, 1993, and Freitas & Oliveira 1992). All measurements were made using a microscope fitted with a calibrated micrometric ocular.

A mark-recapture census for *Heterosais edessa* and 18 other Ithomiinae was conducted from May 1991 to May 1992. Visits were made from 1 to 5 times per week, except from December 1991 to April 1992 (less than once a week). Data on some species were also gathered from 14 January to 11 March 1989. Butterflies were captured with an insect net, individually numbered on the underside of the forewings with a felt-tipped pen, and released at the site of capture. The characteristics of each individual (sex, age, site of capture, source of nectar, and other activities) were recorded for later analysis. The age of individual butterflies was estimated in six categories based on wing wear (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973, Brown et al. 1981, Freitas 1993). Males and females were analyzed separately. Time of residence (permanence) in the population was estimated following Brussard et al. (1974), as days elapsed between marking and last recapture. This parameter is related to the survivorship of the adults.

Rates of flower visitation were recorded during the 12 months of population studies of *Heterosais edessa*. A plant species was classified as highly visited if 50 or more individuals of *H. edessa* were observed feeding on its flowers, intermediate if 10 to 49 individuals were observed, and low if fewer than 10 individuals were observed on it during the entire study (as in Freitas 1993).

RESULTS

Juvenile Biology of *H. edessa*

Drummond and Brown (1987) recorded *Cestrum amictum* Schldl. (Solanaceae) as the larval host of *H. edessa* in coastal São Paulo. In the

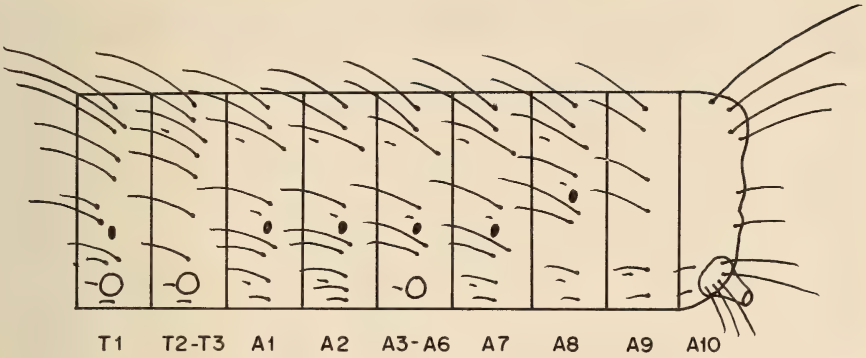

FIG. 1. Distribution of body setae on the first instar larva of *Heterosais edessa*.

Morro do Japuí study site, females followed oviposited only on *Cestrum laevigatum* Schldl. Eggs were laid singly on the underside of old leaves. In general, only one or two eggs were present on each leaf, but as many as six eggs were observed on the same leaf on plants protected from direct sunlight. Although this was not quantified, eggs and larvae were more commonly found on the host plants from April to August.

After hatching, caterpillars ate the entire egg shell. The caterpillars were very sensitive to low humidity and died rapidly in drier environments. Although solitary, larvae were not cannibalistic; several larvae of different instars could be reared together without losses. The caterpillars rested in a J-shaped position on the underside of the leaves. The caterpillars ate all the leaf tissue, even in the first instar. When disturbed, caterpillars could suspend themselves from silk threads, but this behavior was not frequently observed. Pupation usually occurred off the host plant, on neighboring plants but some pupae were found on leaves and stems of *C. laevigatum*.

Egg. White, ovoid (truncated at bottom) with 23 longitudinal ridges and 11 transverse ridges; diameter 0.7 mm, height 0.6 mm. A line drawing of the egg was published by Brown and Freitas (1994).

First instar. Translucent white with transparent head capsule, becoming pale green after feeding; average width of head capsule 0.39 mm (sd=0.02, n=4); distribution of setae as in Fig. 1. Duration 3–4 days.

Second instar. Pale green with a transparent head capsule, dark intestinal contents evident; average width of head capsule 0.58 mm (sd=0.04, n=11). Duration 3–4 days.

Third and fourth instars. Similar to previous instar, with progressively darker green pigmentation; head capsule entirely transparent. Fourth instar larvae with narrow lateral yellow stripe (see also Brown & Freitas 1994). Average width of third instar head capsule 0.9 mm (sd=0.04, n=13); duration 3–4 days. Average width of fourth instar head capsule 1.35 mm (sd=0.05, n=8); duration 3–4 days.

Fifth instar. Green, with narrow lateral yellow stripe (see Brown & Freitas 1994). Head capsule entirely transparent with dark area in ocellar region. Dorsal vessel clearly

TABLE 1. Mark-recapture study of *Heterosais edessa* in Morro do Japuí, Sao Paulo, Brazil. L = maximum longevity, M = maximum movement, m = males, f = females, cap = total, recap = total recaptured.

									Multiple Recaptures				
	CAP		RECAP						males			females	
Month	m	f	m	f	Lm	Lf	Mm	Mf	1	2	3	1	2
May 91	18	2	2	0	3	—	50	—	2	—	—	—	—
Jun 91	11	0	4	0	2	—	100	—	4	—	—	—	—
Jul 91	84	54	17	11	65	21	300	100	14	2	1	11	—
Aug 91	49	33	12	9	23	13	280	100	10	—	2	7	3
Sep 91	7	11	3	6	10	39	100	50	3	—	—	3	3
Oct 91	2	1	0	0	—	—	—	—	—	—	—	—	—
Nov 91	6	1	0	0	—	—	—	—	—	—	—	—	—
Dec 91	1	0	0	0	—	—	—	—	—	—	—	—	—
Jan 92	3	3	0	0	—	—	—	—	—	—	—	—	—
Feb 92	0	0	0	0	—	—	—	—	—	—	—	—	—
Mar 92	0	0	0	0	—	—	—	—	—	—	—	—	—
Apr 92	0	0	0	0	—	—	—	—	—	—	—	—	—
May 92	10	2	1	0	17	—	100	—	1	—	—	—	—
Totals	192	107	37	26	65	39	300	100	32	2	3	21	6

visible. Maximum length 26 mm. Average width of head capsule 2.69 mm (sd=0.21, n=9). Duration 4–6 days.

Pupa. Green, strongly humped (bowed), 0.9 × 1.2 mm; light green first day, acquiring gold stripes after one or two days. A few scattered black dots on wing cases and in ocular area (see Brown & Freitas, 1994). Duration 9 to 11 days.

Adult Ecology of *H. edessa*

In total, 299 adult *H. edessa* were captured during 12 months of study, with 63 later recaptured. Fig. 2 shows individuals present per day; when an individual was recaptured it was considered present in the population on all previous days since the day of first capture. Adults were most abundant from May to September, with abundance decreasing after October and maintaining low population levels during the following months (Table 1). During a short capture period, from January to March 1989, 23 individuals of *H. edessa* were captured on flowers of *Adenostemma viscosum* Forst. (Asteraceae) inside the forest. The population appeared to be breeding continuously, with some peaks (Fig. 2).

The sex ratio of *H. edessa* in the field deviated from 1:1 (197 males and 107 females marked; χ^2=24.2, df=1, p<0.001). Males were the dominant sex throughout the study, except in September 1991 and January 1992 (Fig. 3). The proportions of recapture of males (19.3%) and females (24.3%) can be considered equal (χ^2=0.71, df=1, p>0.20).

For the analysis of age structure, the six initial age categories were grouped into three: new, intermediate, and old (as in Freitas 1993).

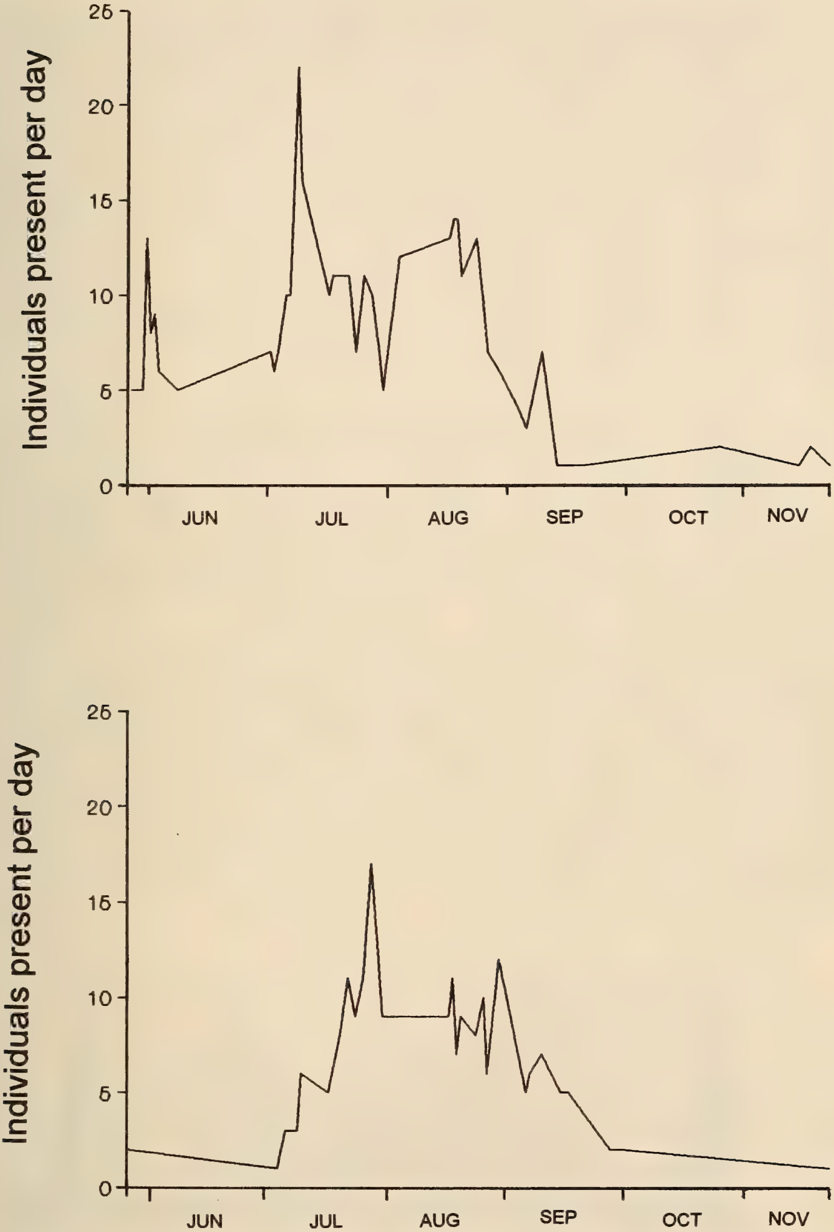

FIG. 2. Individuals of *H. edessa* present per day in Morro do Japuí: males (upper) and females (lower).

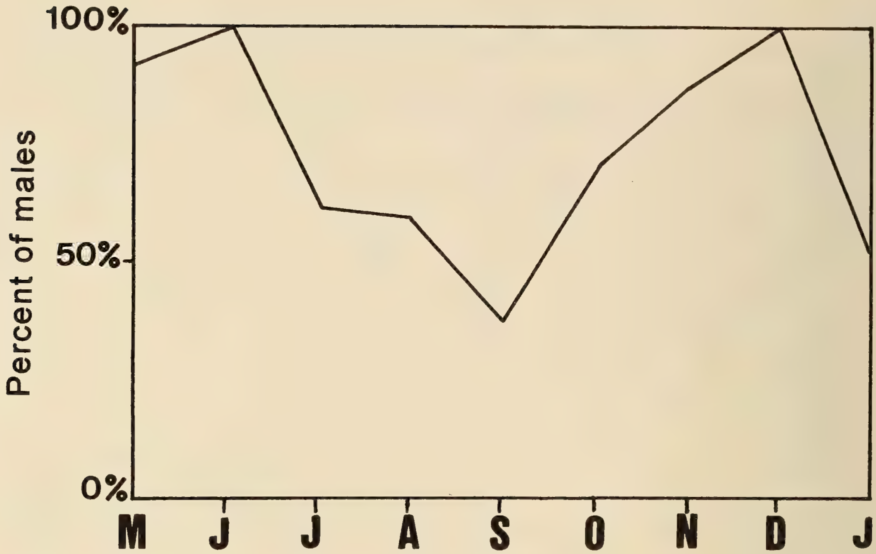

FIG. 3. Sex ratio for *H. edessa* marked in the Morro do Japuí, as percent of males in each day's capture.

Data for males and females were grouped to increase the total data and enhance perception of age patterns along time. The age structure of *H. edessa* was dominated by new and intermediate individuals during most of the study. Old individuals appeared mainly after July, with little increase in number during the following months (Fig. 4). No emergence peaks of new individuals were observed throughout the study, and new individuals reached 100% only on days with only one or two individuals captured.

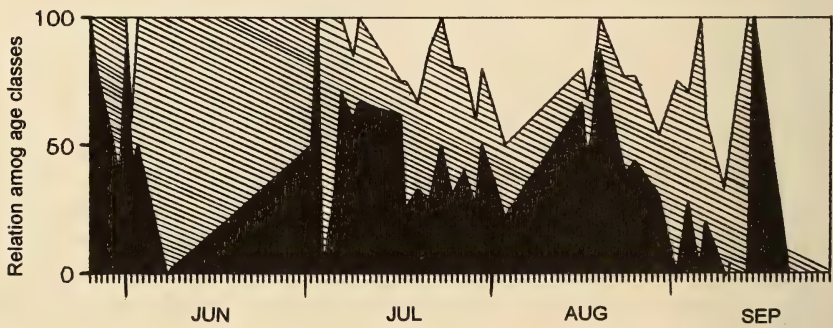

FIG. 4. Age structure of *H. edessa* (males and females grouped) in Morro do Japuí, May to September 1991: black=fresh (new) individuals, hatched=intermediate, white=old, as percent of total for each day.

TABLE 2. Permanance of marked *Heterosais edessa*: days elapsed between marking and last recapture represent the minimum permanance (MP) for each individual.

MP	Males	Females	Total
1–5	16	9	25
6–10	7	5	12
11–15	4	2	6
16–20	3	3	6
21–25	2	5	7
26–30	—	2	2
31–35	1	—	1
36–40	1	1	2
> 40	3	—	3

The movement of adults was limited, and the distance between release site and recapture rarely exceeded 100 m. Of the 63 recaptures, 28 males (75.7%) and 23 females (88.5%) were less than 100 m from the site of first capture, and the other 9 males and 3 females were 100–300 m away. Males had a residence time (12.9 days, sd=15.1, n=37) practically equal to females (13.5 days, sd=10.3, n=26) (Table 2).

Nectar sources utilized by *H. edessa* are available during the entire year, as shown in Table 3. Some individuals were also observed on bird droppings and broken stems of several *Eupatorium* species. Adults were often encountered near a nectar source, but sometimes they were observed flying low inside the forest or near streams and valleys many times away from any nectar source. Adults were frequently found on flowers of Asteraceae, flying erratically near the ground (rarely over 1 m), like other transparent species of Ithomiinae found in the study area (such as *Pseudoscada erruca* (Hew.), *Oleria aquata* (Weymer), *Pteronymia carlia* Schaus, *Hypoleria adasa* (Hew.), *Ithomia drymo* Hübner, *I. agnosia zikani* D'Almeida and *I. lichyi* D'Almeida).

The Ithomiinae Community in Morro do Japuí

Besides *H. edessa* and the seven species mentioned above, another 12 ithomiine species were present in the study area, including: *Melinaea ludovica paraiya* Reakirt, *M. ethra* (Godart), *Placidula euryanassa* (Feld. & Feld.), *Methona themisto* (Hübner), *Mechanitis l. lysimnia* (Fabricius), *M. polymnia casabranca* Haensch, *Epityches eupompe* (Geyer), *Hypothyris ninonia daeta* (Boisduval), *Dircenna dero celtina* (Burmeister), *Prittwitzia hymenaea* (Prittwitz) (one individual in six years), and *Episcada clausina striposis* Haensch. All 12 of these species were also marked and recaptured at the same time as *H. edessa*, but some species were not abundant enough to permit continuous graphs of population dynamics (Fig. 5). Other Ithomiinae found in hills up to 5 km around

TABLE 3. Nectar sources visited by adult *Heterosais edessa* during 1989–1992 in Morro do Japuí, S. Vicente, Brazil. Continuous lines are periods of intense flowering, broken lines indicate few flowers available (1–5 individuals with flowers). Level of visitation of nectar sources: *** = high, ** = intermediate, * = low. *Vernonia condensata* and *Persea americana* are introduced plants in the study area.

Nectar source	J	F	M	A	M	J	J	A	S	O	N	D
ASTERACEAE												
Eupatorium vitalbae D.C. *												
E. laevigatum Lam. ***												
E. punctulatum D.C. *												
E. inulaefolium H.B.K. *												
Mikania lundiana D.C. *												
M. micrantha H.B.K. *												
M. cordifolia (L.F.) Willd *												
Trixis antimenorrhoea Mart. ex Baker **												
Vernonia condensata Baker ***												
V. beyrichii (Less.) *												
V. scorpioides (Lam.) *												
Adenostemma viscosum Forst. ***												
Ageratum conyzoides Linn. *												
Bidens pilosa Linn. *												
Emilia sonchifolia D.C. *												
ROSACEAE												
Rubus rosaefolius Smith. ***												
LAURACEAE												
Persea americana Mill **												
BORAGINACEAE												
Cordia verbenacea D.C. *												

the study area were *Aeria olena* Weymer, *Callithomia lenea* (Cramer), *Thyridia psidii cetoides* (Rosenberg & Talbot), *Pteronymia euritea* (Cramer) and an as yet undescribed subspecies of *Pseudoscada quadrifasciata* Talbot. These five species are probably present erratically in the study site, perhaps even as established colonies, since the foodplants are available and the characteristics of the vegetation are the same as in the adjacent forests. As the São Paulo coast receives rainfall all year round, no Ithomiinae "pockets" were observed during the six years of constant visits to the study area, but some small aggregations were found near streams on hot summer days.

Sex ratios. The sex ratios of all species in the study site were male-biased, except in those species with very few individuals marked (Table 4). The sex ratios showed few changes from month to month, and only *I. drymo* showed a tendency for increase in the number of females during the study (Table 5). The two species of *Melinaea* (studied in 1989), showed an extreme case of male-biased sex ratio (Table 6). During the

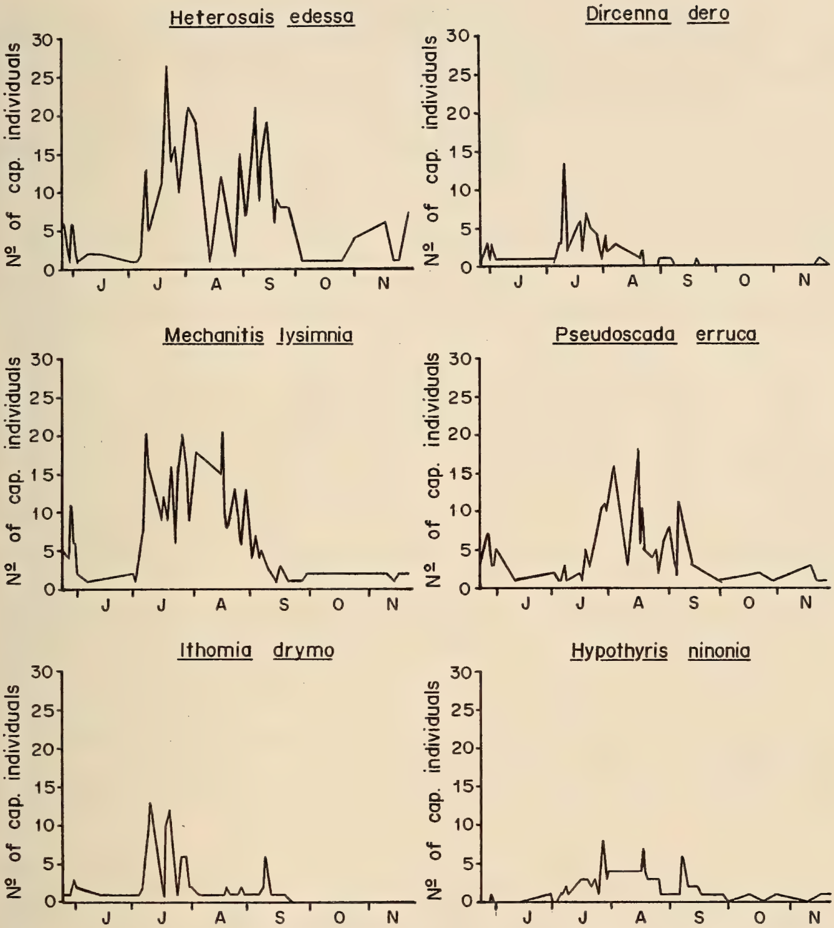

FIG. 5. Individuals of six Ithomiinae species (males and females combined) captured per day in Morro do Japui.

study no females of *Melinaea ethra* and only two of *M. ludovica* were recorded, both flying inside the forest.

Longevity. Permanence in the population (an indirect predictor of life span) was measured only for a few species, due to the low rates of recapture for most. In three species studied in 1991–1992 (*M. lysimnia*, *D. dero* and *H. edessa*) and in the two *Melinaea* studied in 1989, average permanence was typically more than 10 days (though near this in females of *D. dero*), except in *P. euryanassa*, (average less than 10 days; Freitas 1993). In all species studied, maximum permanence was over one month, exceeding two months in some species (Table 7).

TABLE 4. Sex ratios of 18 Ithomiinae species captured in Morro do Japuí, S. Vicente, Brazil, from 26 May 1991 to 26 May 1992. Asterisks indicate sex ratios significantly different ($p<0.05$) from 1:1 using chi-square. Percent total = percentage of all captures represented by that species. Days present = number of days a given species was present during the entire study.

Species	Males	Females	Total	Percent Total	Days present
P. euryanassa *	414	301	715	38.6	50
H. edessa *	192	107	299	16.1	49
M. lysimnia *	182	88	270	14.6	47
D. dero *	90	61	151	8.1	46
I. drymo	64	45	109	5.9	34
M. polymnia *	68	30	98	5.3	33
P. erruca *	48	20	68	3.7	29
H. ninonia *	32	16	48	2.6	20
P. carlia	13	10	23	1.2	19
H. adasa	12	9	21	1.1	15
O. aquata	11	4	15	0.8	12
M. ludovica *	10	2	12	0.6	6
M. themisto	3	6	9	0.5	5
M. ethra *	5	1	6	0.3	4
E. eupompe	1	2	3	0.2	2
E. clausina	1	1	2	0.1	2
I. lichyi	1	1	2	0.1	1
I. agnosia	1	0	1	0.1	1

TABLE 5. Sex ratios for four Ithomiinae species marked in Morro do Japuí, given as percent (boldface) of males in the total (T) for each month.

Species	May T/%	Jun T/%	Jul T/%	Aug T/%	Sep T/%	Oct T/%	Nov T/%
D. dero	14/**71**	6/**83**	40/**57**	35/**51**	23/**52**	3/**67**	5/**60**
M. lysimnia	15/**80**	7/**86**	119/**68**	43/**62**	46/**54**	5/**80**	15/**67**
I. drymo	2/**100**	7/**86**	73/**62**	10/**50**	10/**30**	0/**0**	0/**0**
P. erruca	4/**75**	4/**100**	48/**62**	8/**87**	2/**100**	1/**100**	1/**100**

TABLE 6. Populational parameters for *Melinaea ludovica* and *M. ethra*, 14 January 1989 to 11 March 1989. TM = total marked, TC = total captured, MOV = maximum movement (meters), PER = maximum permanance (days), x = average permanance (with standard deviation), m = males, f = females. All males collected were feeding on *Adenostemma viscosum*.

	TM		TR	MOV	PER		Multiple recaptures			
	m	f	m	m	m	x	1	2	3	4
M. ludovica	113	2	32	300	55	14.1 ± 14.1	25	5	2	0
M. ethra	115	0	33	300	47	13.7 ± 12.9	25	4	2	2

TABLE 7. Permanence in the population for four species of Ithomiinae studied in Morro do Japuí, 1991–1992. x = average permanance (days, with standard deviation).

Species/sex	x	range	SD	N
P. euryanassa males	8.4	1–45	8.3	149
P. euryanassa females	7.2	1–23	5.7	112
M. lysimnia males	15.5	1–67	15.4	72
M. lysimnia females	18.3	1–72	16.2	31
D. dero males	9.4	3–23	6.9	21
D. dero females	10.9	3–49	10.5	23
H. edessa males	12.9	1–65	15.1	37
H. edessa females	13.5	2–39	10.3	26

All species studied showed a peak of abundance between July and August (Figs. 2, 5; see also Freitas 1993 for abundance graphs of *P. euryanassa*), except the two *Melinaea* species, which were most abundant from November to March (summer months); in 1991–1992 they were not as abundant as in 1989 and 1990.

Food sources. Adult Ithomiinae were usually observed on flowers, especially of Asteraceae (Table 8). Nectar sources in the study site were available all year round (Table 3). All species showed a preference for flowers in the Asteraceae, except the transparent blue Ithomiinae species (*H. edessa*, *I. drymo*, *I. lichyi*, *I. agnosia*, *P. erruca*, *P. carlia* and *O. aquata*), that prefered flowers of *Rubus rosaefolius* (Rosaceae), all year (Table 8; other transparent blue species not present in the Table were also captured mostly on these flowers: *H. adasa*, 17 of 22 feeding records; *P. carlia*, 12 of 23; *O. aquata*, 6 of 7). The apparent strong pref-

TABLE 8. Frequency of flower visitation for 8 species of Ithomiinae studied in Morro do Japuí, 26 May 1991 to 16 May 1992. Plants with an asterisk are known PA sources. Bold numbers indicate that visitation is male biased. Results presented as males/females. See Table 3 and text for full names of plants and butterflies (*A.cura.* = *Asclepias curassavica*).

	Pla. eur.	*Mec. lys.*	*Mec. pol.*	*Dir. der.*	*Het. ede.*	*Ith. dry.*	*Hyp. ada.*	*Pse.* err.
E.laev. *	**81/34**	**27/4**	30/19	**34/11**	**24/4**	2/0	4/0	0/1
E.punc. *	2/0	—	1/0	1/0	1/0	—	—	—
M.lund.	4/2	0/1	—	3/1	1/3	2/2	—	—
T.anti.	24/13	3/4	—	2/0	6/3	8/9	—	3/4
V.cond.	**167/111**	**61/33**	2/1	45/56	31/30	6/2	11/10	4/2
R.rosa.	23/15	36/29	0/1	8/9	**106/74**	32/26	15/16	**34/14**
P.amer.	274/265	27/28	—	16/16	6/12	3/2	4/3	—
C.verb.	13/7	4/4	—	3/0	0/1	2/0	—	—
A.cony. *	0/1	1/0	—	—	—	—	—	—
V.scor.	0/1	1/0	—	—	—	—	—	—
A.visc. *	—	3/0	6/0	—	1/1	—	—	—
A.cura.	—	—	1/0	0/1	—	—	—	—

erence of *P. euryanassa* for flowers of *Persea* (Table 3) may have been due to chance, since this seemed to be the most abundant flower during the population peak of this species (Freitas, 1993). In general, the records of males and females were near 1:1 on all nectar sources. On *E. laevigatum* males were more abundant for most of the species. In 1989, *Adenostemma viscosum* also attracted mainly males of *Melinaea* (Table 6), as well as *H. edessa* (25 males and no females) and *O. aquata* (21 males and 1 female). Adult Ithomiinae individuals of both sexes were also observed puddling on mud, and feeding on bird droppings, rotting fruits, and broken stems of several *Eupatorium* species.

Species composition. Data on relative species abundance were analyzed only for the period from 26 May to 23 November 1991, when individuals were most abundant and the censuses were more frequent. Throughout this period, four species (*P. euryanassa*, *H. edessa*, *M. lysimnia* and *D. dero*) accounted for at least 70% of the captured Ithomiinae on any day (see also Table 4 and Fig. 6A). The number of species captured per day varied from 2 to 13 (mean 6.96, sd=2.6, n=54), with at least 6 species present on most days (Fig. 6B). The most abundant species were also the ones that were seen on most days (Table 4), showing that they were well distributed throughout the year (see also Fig. 5, and Freitas 1993). The days with more than six species captured were mostly in July and August, also the period when the largest number of individuals were seen per day (Fig. 6B). The abundance of some species varied from year to year: *Ithomia lichyi* was very abundant in 1989 and 1990, but *I. agnosia* and *E. clausina* were always sparse from 1988 to 1993. Some abundant species may be rare in other years: *Pseudoscada erruca*, a moderately common species from 1988 to 1993, was practically absent in the first part of 1994 in Morro do Japuí, although it continued to be common in other forests near the study area.

DISCUSSION

Biology of *H. edessa*

Heterosais edessa has immatures typical for its tribe (Godyridini), with solitary larvae, little pigment in the larval cuticle including cephalic capsule, and a bent, green pupae; all these are considered derived traits in the Ithomiinae (Brown & Freitas 1994). Although larvae are solitary, they do not exhibit cannibalistic habits, common in solitary larvae of Heliconiini (Brown 1981 and pers. obs.). Several other Ithomiinae with solitary larvae were also not aggressive towards other smaller larvae (pers. obs.); this trait may have allowed the development of gregarious behaviour in Ithomiinae larvae. In fact, gregarious larvae are considered to be a polyphyletic trait in Ithomiinae, appearing erratically in many Ithomiinae radiations (see Brown & Freitas 1994).

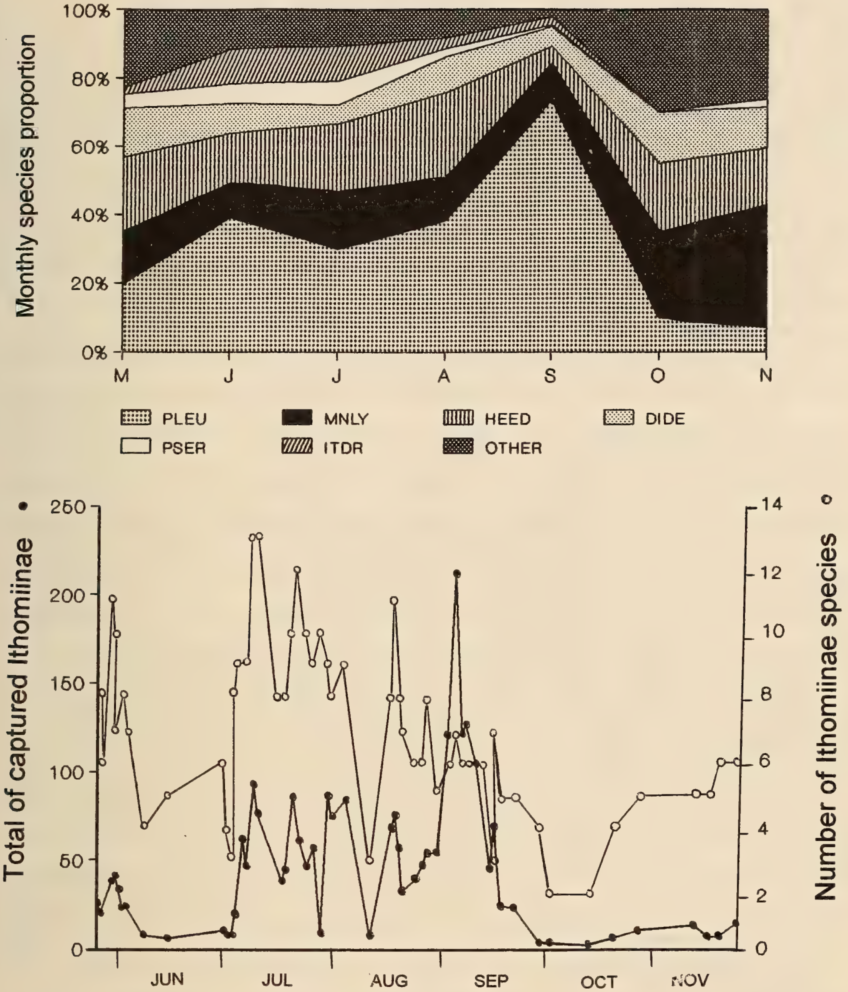

FIG. 6. Upper: species ratio of Ithomiinae captured in Morro do Japuí from May to November 1991. Bottom: total of individuals of all Ithomiinae captured in Morro do Japui from May to November 1991 (filled circles) and number of Ithomiinae species captured per day in the same period (open circles).

The general behavior of *H. edessa* larvae, like the J-shaped resting position and the suspension by silken threads when disturbed, is very similar to that of other known Ithomiinae (Brown & D'Almeida 1970, Young 1972, 1974a, 1974b, 1974c, 1978a, 1978b, Ackery 1987). Larvae of *H. edessa* are basically cryptic in color pattern and behavior.

The Ithomiinae Community of Morro do Japuí

Although more abundant in the winter months, *H. edessa* is found in Japuí all year round; the low numbers in some months may be due mostly to the low number of plants in bloom. This pattern of fluctuation seems to be present in varying degrees in most Ithomiinae (Vasconcellos-Neto 1980, Freitas 1993). The vagility of *H. edessa* is low, with individuals usually tracking their nectar sources. Because the larval food plants are present throughout the area, females do not need to search widely to find them, so both male and female movement is more related to nectar sources.

Sex ratio was male biased in *H. edessa* and seven other ithomiine species. Male biased sex ratios in the field have been reported for many species of butterflies, even when sex ratio in the laboratory was 1:1 (Brussard & Ehrlich 1970, Brussard et al. 1974, Brown & Ehrlich 1980, Matsumoto 1984, 1985, Freitas 1993). In the Ithomiinae, the predominance of males in field collections has been attributed to their appearance at sources of pyrrolizidine alkaloids (PAs) (Brown 1985, Trigo 1988, Freitas 1993), as seen with *E. laevigatum* in this study. The fact that male biased sex ratios were also detected on other plants (e.g., *R. rosaefolius*) may be explained by the existence of behavioral differences between males and females (Ehrlich 1984), resulting in males generally flying in the same places as the collectors, with females more dispersed throughout the habitat.

The residence times of *H. edessa* and the other Ithomiinae in the study area were relatively high compared to species in other butterfly families, but were lower than those for species of *Heliconius* in the same area (Rogner & Freitas, unpubl. data). Some individuals may survive for more than two months, and two females older than 30 days were observed ovipositing and with apparently distended abdomens, indicating continual egg production as in *Heliconius* species (Dunlap-Pianka et al. 1977). The relatively short lifespan of Ithomiinae in this study site in relation to that in other regions (Vasconcellos-Neto 1980, Brown 1985) may be due to the continuously humid climate, and concomitant lack of reproductive diapause in this region. The age structure of adult *H. edessa* shows that the population has continuous recruitment of new individuals throughout the year, though probably diminished from July to December. These data suggest that *H. edessa*, like most other Ithomiinae in the study site, is more K-selected (Pianka 1970) than *Placidula euryanassa* (Freitas 1993).

The Ithomiinae community in Morro do Japuí is typical for the São Paulo coastal region. The absence of montane species results in a low richness in relation to the interior (28 species in the "Serra do Japi," in-

terior of São Paulo; Brown 1992), although some species like *H. edessa* are absent in the interior, or occur only as migrants from the coast (the two *Melinaea* and *O. aquata*). Also, several species in the coastal Atlantic transparent yellow complex (Brown & Benson 1974) are absent in the region (like *Scada karschina*), appearing only 100 km east of São Vicente in São Paulo state (São Sebastião municipality).

The number of species captured per day throughout the year was almost always more than six, reaching 13 on some days, with high numbers of individuals, reflecting a relatively high diversity. Eleven species are common enough to be captured on almost any day in the study site. A relatively complete list of Ithomiinae of a given coastal São Paulo site may be obtained in four to five days of intense work from June to September, especially with the use of *Heliotropium indicum* baits to attract males of rarer species, or by searching for the right flowers (habitat "pockets" that concentrate adult Ithomiinae in winter are virtually absent in most of the São Paulo coastal region; see also Brown 1972). A survey of the 26 Ithomiinae species of São Sebastião was made in only seven collecting trips from May to September 1992.

The data presented here provide valuable information for two kinds of community studies. Firstly, the study of plant-based food webs is of great importance in the understanding of tropical ecosystems. For example, the data obtained for a given taxonomic group of herbivorous insects can be useful in studies of diversity and health of a given plant assemblage. This is especially true for groups like Ithomiinae which are rapidly sampled and depend on a diverse set of plants for larval and adult hosts (Gilbert 1980). Ithomiinae have been suggested as especially good indicator organisms for this kind of study (Brown 1991, Beccaloni & Gaston 1995). Secondly, an understanding of the seasonal patterns of each species, as well as their behavior, habits and preferences can lead to greater efficiency in collecting data in a given area, especially if many areas must be surveyed in little time. Some sites are difficult to reach, so that the knowledge of which months are better to census butterflies is valuable to those who intend to carry out inventory and monitoring.

The present paper attempts to define some of these patterns for the São Paulo coastal forests, to help future work in this region. Similar work is needed in other areas to reveal the different patterns, especially in places with marked seasonality or with different climatic regimes.

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OVIPOSITION BEHAVIOR AND LARVAL BIOLOGY OF THE ENDANGERED UNCOMPAHGRE FRITILLARY *BOLORIA ACROCNEMA* (NYMPHALIDAE)

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ABSTRACT. *Boloria acrocnema* is an endangered relict arctic nymphalid restricted to fewer than five mountain peaks in Colorado, USA. Females lay eggs singly on snow willow, *Salix reticulata nivalis* (Salicaceae), and eggs hatch 23 to 32 days later. The larvae are most likely biennial and pass though one to possibly two instars before overwintering. However, evidence of an annual life cycle is also presented. Later instar larvae break diapause in mid to late June and feed on snow willow leaves. Pupation occurs in the host plant litter and adults emerge 21 to 32 days later.

Additional key words: annual life cycle, biennial, immatures, Salicaceae.

The Uncompahgre fritillary, *Boloria acrocnema* Gall and Sperling (Nymphalidae) was discovered in 1978 on Mt. Uncompahgre in the San Juan Mountains, Hinsdale County, Colorado, and subsequently described by Gall and Sperling (1980) as a new species. Three active colonies of the species were known during the course of this study: a colony at Mt. Uncompahgre, the type locality (UP1); a colony approximately 4 km southwest of the type locality (UP6); and a colony on Redcloud Peak approximately 20 km SSE of the type locality (RC1). Both sites are on or are adjacent to public lands; RC1 is located within Bureau of Land Management (BLM) lands, and UP6 exists just outside the Big Blue Wilderness Area of the Uncompahgre National Forest. Extensive searching during 1988 led to the discovery of two additional locations, but butterfly numbers were low and they were not considered breeding colonies (Brussard & Britten 1989). During the 1995 flight season, however, Colorado Natural Heritage Program biologists confirmed the presence of butterflies at these locations and at another location in the La Garita Mountains (Aaron Ellingson, pers. comm.). Additionally, a private collector has reported the location of another colony (Paul Opler, pers. comm.). Total colony number is now seven.

Boloria acrocnema, in similarity with some other alpine butterflies, is considered but not confirmed to have a biennial life cycle, wherein each brood overwinters twice and development occurs over three summers, thus creating odd- and even-year populations (Scott 1982, 1986, Brussard & Britten 1989). The larvae of *B. acrocnema* feed on a single

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host plant, snow willow, *Salix reticulata* L. spp. *nivalis* (Hooker) Love (Salicaceae), a species common in mesic alpine environments (Weber 1987).

The species' larval life history has been studied in the laboratory by Scott (1982). Here, I report on the larval life history of *B. acrocnema* as described from 3 years of field observation. I suggest that some *B. acrocnema* individuals complete their life cycle in a single year i.e., during two summers, and discuss how a "staggered" dynamic may affect the results of demographic studies for this endangered butterfly.

STUDY SITES AND METHODS

Research was conducted from 1991–1993 at two of the three known *B. acrocnema* colony sites, RC1 (37°57'N, 107°25'W) and UP6 (38°04'N, 107°25'W). Both sites exist on slopes with a northeast exposure and range in elevation from 3800–3970 m, with UP6 lower than RC1. Each site has abundant patches of *S. reticulata nivalis*, the larval host plant, and both have a variable array of nectar sources including *Erigeron vagus* Payson (Asteraceae), *E. simplex* Greene (Asteraceae) and *Silene acaulis* L. ssp. *acaulescens* (Williams) Hitchcock and Maquire (Caryophyllaceae), the most commonly used nectar sources by *B. acrocnema* (Seidl 1995). The sites differ in area: RC1 is approximately 10 ha, and UP6 is approximately 1.2 ha.

Female *B. acrocnema* were followed during 1991–1993 at RC1 and UP6 to locate oviposition sites. Females were followed by an observer at a distance of approximately 3 m. If an oviposition was observed, the location was marked with a survey flag and then searched for eggs. Leaves on which an egg was deposited were classified as to stage and development. Records were kept of how well the egg was adhered to its substrate, each egg's development and changes in color and ridge shape. Finally, a record was kept of whether the egg hatched or if it became desiccated or otherwise appeared infertile. Egg locations were marked with an aluminum tag and a metal stake and were returned to the following summer to search for developing larvae.

In 1992 and 1993 a total of five late third and fourth instar larvae were found, described and placed in enclosures. Although these larvae were found near marked oviposition sites, none were seen at the exact location of the previous summer's oviposition sites. In 1992, each larva was enclosed within snow willow habitat in a 1 m × 1 m × 15 cm lidded wood-screen enclosure. In 1993, each larva was enclosed in an unlidded Lexan (similar to Plexiglas) enclosure of the same dimensions. The glass-like surface of the Lexan prevented caterpillars from escaping. The Lexan design proved to be more similar to natural conditions i.e., air temperature and exposure to precipitation. Activity, development and

morphology of larvae, especially as they developed into pupae and then into adults, were noted.

RESULTS

Oviposition behavior. In 1991 follows were conducted from July 17 to August 9 and ovipositions were seen July 17 to August 2. In 1992 follows were begun July 8 to August 4 and ovipositions were seen July 14 to August 4. Finally, in 1993 follows were begun June 30 to August 6 and ovipositions were seen during that same period. Sixty-four oviposition sites were found during the 1991–1993 field seasons. Fourteen eggs were laid on the underside of *Salix reticulata nivalis* leaves, 14 eggs were laid at the base of a leaf or on the petiole, 13 eggs were laid on the top side of the leaf, 11 were laid on *Salix reticulata nivalis* leaf litter, 2 were laid at the base of a *Salix reticulata nivalis* plant, 1 was laid on the stem of a catkin and the remaining 9 were laid within *Salix reticulata nivalis* habitat but on different plants, including grass, moss, *Erigeron* spp., *Silene acaulis*, and *Salix arctica* Pallas (Salicaceae). Female *B. acrocnema* preferred opened *Salix reticulata nivalis* leaves to unopened: of the 55 ovipositions on *Salix reticulata nivalis* only one was recorded on an unopened leaf.

Female *B. acrocnema* often walked among *Salix reticulata nivalis* patches testing leaves (abdomen extended toward leaf but no egg deposited) before actually ovipositing. For the follows conducted during 1991 and 1992, I recorded testing behavior as well as oviposition behavior. In 1991, 4 of the 18 ovipositions recorded were directly preceded by testing. In 1992, 8 of the 15 ovipositions recorded were preceded by testing.

The eggs, when first laid, are cream colored and become pink to tan or grey after 3–5 days. All eggs were closely observed and their development was followed until they either fell to the ground or into the litter and were lost, hatched into first instar, or appeared dead or desiccated. Many of the eggs were not well cemented to *Salix reticulata nivalis* plant material. Of the 64 ovipositions recorded, 41 fell preventing further observations. An additional 6 eggs became desiccated and 13 showed development but no hatching by the end of the study. No first instar larvae were seen in 1991, and early winter snowfall in 1992 prevented further observations. In 1993, however, there was evidence of 4 eggs having hatched: 2 first instar larvae were actually seen emerging from their eggs (Fig. 1) and 2 other egg casings showed signs of recent hatching. The period between oviposition and hatching ranged from 23 to 32 days (July 25 to August 16 and July 20 to August 20, respectively).

Larval Life History. Five third and fourth instar larvae (Fig. 1) were identified using criteria from Scott (1982) and followed in the enclosures to adult emergence during 1992 and 1993. Of those 5, three lar-

FIG. 1. Immature stages of *Boloria acrocnema*. Clockwise from top left: first instar and egg casing, third instar, pupa, fourth instar.

vae successfully produced adults, while 2 died of unknown causes. In 1992, larvae were found on June 29 and July 2, and in 1993 a single later instar larva was found July 7. All later instar larvae were found at RC1 near oviposition sites, determined the previous summers. Caterpillars were observed feeding and basking for 2–3 days before nesting (larvae make a leaf shelter) and pupation. During the hours prior to nesting, larvae were observed to move rapidly around the enclosures and appeared to test areas for possible pupation sites. This behavior included crawling under litter, beginning to make a nest and then arresting movement. Finally, each caterpillar chose a site with densely packed litter and nested. In one case the larva burrowed under a large dead leaf and attached itself horizontally to the underside of the leaf, silking together debris (dead leaves, lichens, and bits of grass) to form a nest. No movement occurred after nesting and pupation began. In 1992, adults eclosed on August 2 and on August 7. Both of these larvae had pupated on July 7 (Fig. 1). In 1993, pupation was observed on July 9 and the butterfly eclosed on July 29. Therefore, in 1992 and 1993 the duration of pupation was 21 to 32 days.

```
                            Apr   May    Jun    Jul    Aug    Sep
--------------------------------------------------------------------
Annual Life Cycle

  egg                                           |------|
  1st instar                                           |------|
  3rd instar                                                  |---->
  5th instar                             |------|
  pupa                                          |------|
  adult                                                |----------->

Biennial Life Cycle

  egg                                           |------------------>
  1st instar                             |------|
  3rd instar                                    |------------------>
  5th instar                             |------|
  pupa                                          |------|
  adult                                                |----------->
--------------------------------------------------------------------
```

FIG. 2. Hypothetical timeline of annual and biennial development for *Boloria acrocnema* if egg is oviposited during late June during any given year.

Salix reticulata nivalis was the only observed larval host plant, and *B. acrocnema* may be restricted to this species. Pre-pupating caterpillars consumed the top or apex of each unopened leaf. As the leaves developed and opened, the missing apex of each of the three leaves was evident.

Boloria acrocnema larvae typically ate large sections taken from the top of the leaf and often from the tops of all unopened leaves, as described above. Feeding damage on either side of a leaf and single bites in the center of the leaf were also observed. There was one brief instance of a caterpillar eating a *Salix reticulata nivalis* root just prior to nesting.

DISCUSSION

Singly-laid eggs and solitary larvae are characteristic in many *Boloria* species; haphazard egg laying is also characteristic of nymphalid butterflies (Scott 1986), most notably *Speyeria*. The choice of oviposition sites, nearly always on *Salix reticulata nivalis* and almost never on the closely related and equally abundant *Salix arctica*, is intriguing. *Salix* species are known to contain the phenolic compounds salicin and salicortin as feeding deterrents against herbivores (Palo 1984). Future physiological and chemical studies of *Salix arctica* and *Salix reticulata nivalis* and their corresponding levels of phenols may clarify why *B. acrocnema*'s association to *Salix reticulata nivalis* is so specific.

A previous study of larval development of *B. acrocnema* determined the duration of the egg stage to be 10–15 days, with an estimate for first

instar to adult being approximately 42 days (Scott 1982). The data provided here suggest that although a biennial life cycle is probably the typical timespan, an alternative annual cycle is also possible. For instance, in 1993 ovipositions were observed on June 29 at RC1 (Fig. 2). The time from egg stage until hatching was determined to range from 23 to 32 days in the field. An egg laid in late June or early July could have the time to develop into a first instar larva by July 30 and into a third instar that same summer, usually having more than a month to develop before *Salix reticulata nivalis* leaves become senescent and the first snows arrive. The following year (Fig. 2) third instars develop through fifth instar, pupation and eclosion.

Brussard (1991) reasoned that *B. acrocnema* individuals may be staggered such that some butterflies develop in 2 years and others in 3 or more years, depending on the varying ecological conditions (rainfall, air temperature, quality of host plant). Brussard and Britten (1989) used the term "leakage" to describe how even-year brood individuals may, by completing their life cycle in 3 years, become members of the odd-year brood, or vice versa. It is suggested here that some individuals may develop in a single year creating a scenario similar to what Brussard (1991) described.

Variable developmental time spans may result in inaccurate demographic data if a biennial life span is assumed. Because *B. acrocnema* is an endangered species and is the subject of a recovery plan, population fluctuation and demographics play a central role in assessing the species' status. The accuracy of indexes of abundance or population estimates is essential. Currently, *B. acrocnema* demographic studies describe population estimates for odd- and even-year broods (Brussard & Britten 1989, Britten et al. 1994, Seidl 1995). Laboratory studies which would manipulate natural conditions and time phase relationships between *B. acrocnema* and *Salix reticulata nivalis* are needed to assess the proportion of individuals likely to complete their life cycle in a single year. An equation which calculated this proportion would give us a more precise index of abundance or population estimate by which to judge the status of this endangered butterfly.

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NATURAL PUPATION SITES OF THREE NORTH AMERICAN SWALLOWTAIL BUTTERFLIES: *EURYTIDES MARCELLUS* (CRAMER), *PAPILIO CRESPHONTES* CRAMER, AND *P. TROILUS* L. (PAPILIONIDAE)

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ABSTRACT. Pupation sites were determined by releasing wandering prepupal larvae marked with fluorescent paint in a natural area during the day and searching with a UV spotlight the following night. Two of the species studied have environmentally cued pupal color dimorphism: *E. marcellus*, which pupates preferentially on the undersides of leaves, both living and dead, and *P. troilus*, which prefers slender stems among leaves, either living or dead. *Papilio cresphontes* has monomorphic pupae resembling dead wood and prefers pupation sites on dead sticks and woody stems. Together with previous studies, these results support the hypothesis that pupal color determination in swallowtails has evolved in relation to pupation site preference.

Additional key words: pupal color, environmentally cued dimorphism.

Swallowtails, among other groups of butterflies, vary in the ability of their prepupal larvae to respond to environmental cues at their pupation sites. Some species have environmentally cued pupal color polymorphism, with green or brown the most common alternatives, while other species have monomorphic green or brown pupae (Clarke & Sheppard 1972, West et al. 1972, Wiklund 1975, Smith 1978, Hazel & West 1979). The term 'brown' includes shades of gray and really means that the pupa does not resemble a green leaf in its reflectance spectrum. Brown pupae may be variable in color, and in some species may be tinged with dark green (as in *Papilio anchisiades* Fabr., Tyler et al. 1994), but green pupae are usually quite uniform.

We have hypothesized that pupal color determination has evolved in relation to pupation site preference (Hazel & West 1979) and have shown that selection by primarily non-visual predators can drive the evolution of the latter (West & Hazel 1982). The hypothesis predicts that species with sites that are inherently variable in color (for example, leaves or weed stalks that may be alive or dead) will tend to evolve pupal color dimorphism, while monomorphism is expected in species with inherently uniform sites (for example, dead wood in the leaf litter for a brown species, or leafy twigs of evergreen shrubs and trees for a green species).

A major problem testing the hypothesis is the lack of reliable information about pupation sites and pupal colors. We have described pupation sites and pupal colors of *Battus philenor* (L.), *Papilio glaucus* L. and *P. polyxenes* L. (West & Hazel 1979, Hazel & West 1979) and of *P. eurymedon* Lucas (West 1995), from experimental data. Pupal colors have also been described for two other North American species with environmentally cued pupal color, *Eurytides marcellus* (Cramer) (West & Hazel 1985) and *Papilio troilus* L. (Igarashi 1979). We report here experiments on the pupation sites of these two species and of *Papilio cresphontes* Cramer, which has monomorphic pupae (Tyler et al. 1994: 105).

MATERIALS AND METHODS

The insects used in this study were obtained from field-collected larvae and eggs, and from the eggs of field-collected females or those reared and hand-paired in the laboratory. All material originated in Montgomery and Giles counties, Virginia. Larvae were reared in plastic boxes on natural midsummer daylength and temperature and were fed leaves of their local food plants. The experiments were carried out in Blacksburg, Virginia in the summers of 1978 and 1979. The larval food plants of all three species occur locally chiefly in forest understory and along forest edges. They are pawpaw, *Asimina triloba* (L.) Dunal (Annonacaeae), for *E. marcellus*; spicebush, *Lindera benzoin* (L.) Blume, and sassafras, *Sassafras albidum* (Nutt.) Nees (Lauraceae), for *P. troilus*; and hoptree, *Ptelea trifoliata* L., and prickly ash, *Zanthoxylum americanum* Mill. (Rutaceae), for *P. cresphontes*.

To determine the natural pupation sites we used UV-fluorescent paint (West & Hazel 1979). As larvae voided their guts and entered the prepupal stage during the day, they were marked with paint and released in one of three study areas: 'forest,' and two areas of 'edge.' The study areas are described in West & Hazel (1979). In general, the 'forest' area was dominated by trees, with ground cover of dead leaves and sticks and some sparse vegetation. The 'edge' areas were between the 'forest' and an adjacent meadow and had ground cover of tall grasses and weeds as well as saplings. In each area all larvae were released on the same branch of a small tree. Prepupal larvae were located that evening by searching the study areas with a UV spotlight, from the ground to several meters high in the trees. The type of pupation site and its height from the ground were noted, and except for pupations on the undersides of leaves, the diameter of the site was measured at the point of girdle attachment. For dimorphic species, pupal color was recorded after pupation.

Success in finding marked prepupae varied. For *E. marcellus* and *P. troilus* it was about 70%, but for *P. cresphontes* only about 35%. We believe that the low recovery rate, especially of *P. cresphontes*, was due pri-

TABLE 1. Pupation sites of *Papilio cresphontes*, *P. troilus* and *Eurytides marcellus* during the summer in a natural environment. Distributions are different for the three species (χ^2=72.0, df=4, p<0.01).

Species	Pupation site: Dead sticks or living stems, diam.≥0.5 cm	Pupation site: Dead sticks or living stems, diam.<0.5 cm	Pupation site: Leaves
P. cresphontes	11	4	0
P. troilus	0	20	2
E. marcellus	1	3	19

marily to predation on wandering larvae, as fluorescent remains of larvae were often found in the evening on the ground. Once the prepupae had hung up, there was very little loss from predation.

RESULTS

Pupation sites are given in Table 1. *Papilio cresphontes* larvae wandered up to 5 m from the release tree before choosing a site on a broad dead stick or other woody surface above the leaf litter. Eleven of 15 sites were on dead branches more than 0.5 cm in diameter, and the remainder on dead weed stalks and woody stems of the vine *Parthenocissus quinquefolia* (L.) Planchon (Vitaceae). *Papilio cresphontes* has monomorphic brownish pupae resembling lichen-covered twigs, with greenish-grey thoracic and abdominal saddles. *Papilio troilus* larvae moved up to 6 m from the release tree and chose slender stems (20 of 22 sites less than 0.5 cm in diameter) among green or brown leaves. *Eurytides marcellus* larvae moved as far as 3 m, and 19 out of 23 of them chose sites on the undersides of leaves, either living or dead.

DISCUSSION

Taken together with our earlier data (West & Hazel 1979), these results suggest that species with dimorphic pupae (*B. philenor*, *E. marcellus*, *P. polyxenes*, *P. troilus*) use inherently variable pupation sites, but that the variability is in spite of differences among species in the types of sites that they choose. For example (Fig. 1, Table 2), these four species show distinct differences in height above ground, in type of substrate (leaves or stems) or in the width of the substrate, yet in all cases the substrate or its immediate surroundings may or may not be colored by the chlorophylls and xanthophylls of living leaves. The monomorphic species (*P. cresphontes*, *P. glaucus*) also differ somewhat in their sites, but both use exclusively woody substrates.

Among swallowtails, pupal color dimorphism has probably evolved from monomorphic brown (Hazel & West 1995, from physiological evi-

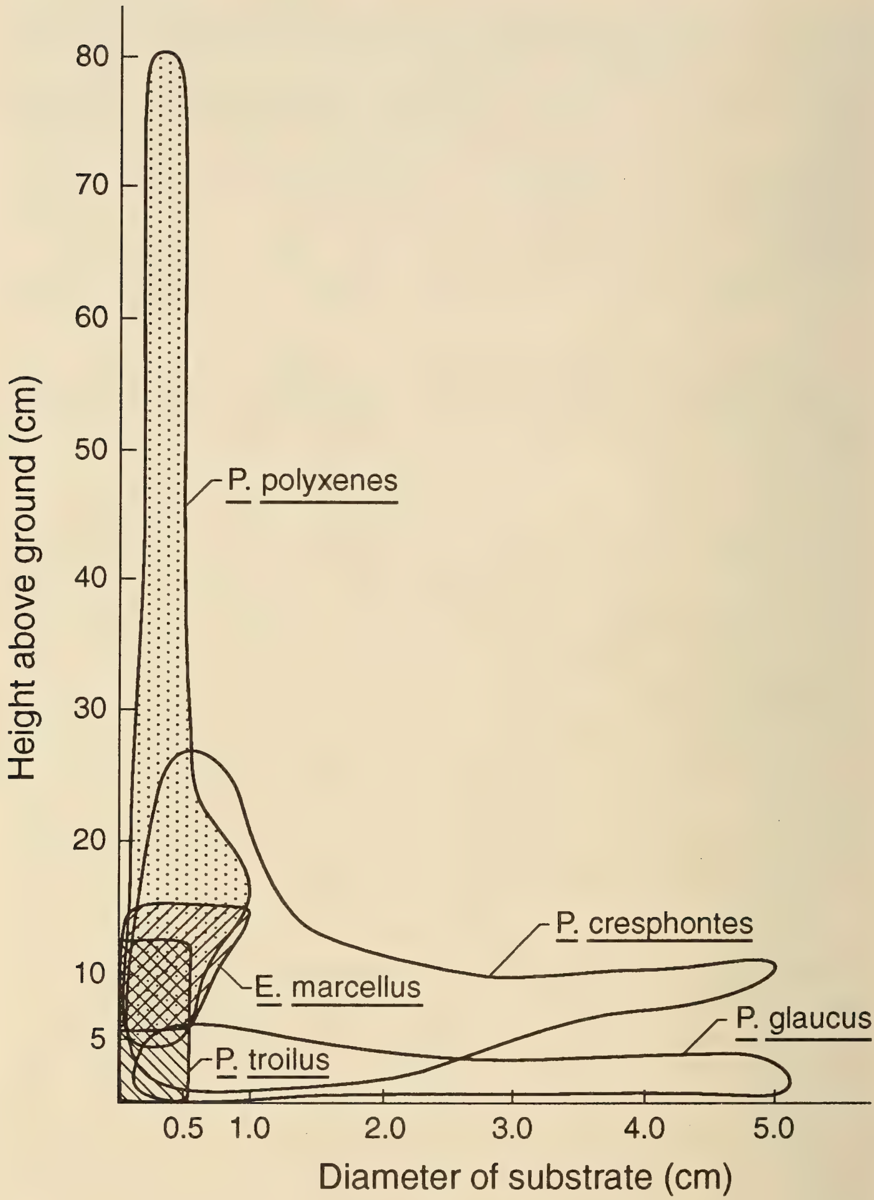

FIG. 1. Ranges in the diameter and height above ground of natural pupation sites of five sympatric swallowtails of eastern North America during the summer generation. The outlines enclose about 95% of the pupations. For pupations on leaves (*Eurytides marcellus* and *Papilio troilus*) only height is given. A sixth species, *Battus philenor*, pupates on vegetation higher than about 90 cm and scarcely overlaps these distributions, but on cliffs may be from 15 cm to several m above the ground or the nearest ledge.

TABLE 2. Variation in pupation sites and pupal color of six eastern North American swallowtails. Data for *Papilio polyxenes*, *P. glaucus* and *Battus philenor* from West & Hazel (1979).

Species	Pupal color	Pupation sites
P. polyxenes	dimorphic	living or dead weed stalks, or woody surfaces above the ground
P. troilus	dimorphic	very slender stems among green or brown leaves close to ground level
B. philenor	dimorphic	tree trunks, cliffs and slender stems well off the ground
E. marcellus	dimorphic	undersides of green and brown leaves close to ground level
P. glaucus	monomorphic brown	undersides of dead sticks or leaves in the leaf litter
P. cresphontes	monomorphic brown	woody surfaces off the ground

dence; but see West 1995, for another view based on genetic evidence). The evidence that it has evolved independently several times is that both monomorphism and dimorphism are found within species groups of the major tribes of swallowtails. In the *glaucus* group of the Papilionini, for example, most species have monomorphic brown pupae, but *P. eurymedon* is dimorphic (West 1995). In the *marcellus* group of the Leptocircini, *E. marcellinus* (Doubleday) has monomorphic brown pupae and pupates in curled-up dead leaves (Turner, *in* Collins & Morris 1985), whereas *E. marcellus* is dimorphic. In the Troidini, some *Battus* species are dimorphic, for example *B. belus* (Cramer) and *B. crassus* (Cramer) (Tyler et al. 1994), and others are monomorphic green (e.g., *B. lycidas* (Cramer)) (Moss 1919). Among Old World troidines, at least some *Troides* spp. are dimorphic, but all members of *Ornithoptera* appear to be momomorphic brown (Igarashi 1979).

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A NEW SUBSPECIES OF *XYLOPHANES TERSA* (SPHINGIDAE) FROM VENEZUELA

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ABSTRACT. A new sphingid subspecies, ***Xylophanes tersa chaconi,*** is described and illustrated on the basis of 16 males from the State of Amazonas, Venezuela. The new subspecies differs from *X. tersa tersa* (Drury) mainly by its dark ash-brown appearance (including postmedian spots of hindwing). *X. tersa chaconi* is strikingly similar in color pattern to an as yet undescribed species from the neighboring State of Bolivar, but the latter has well-defined, cream-colored postmedian spots on the hindwing and slightly different genitalia. Some general biogeographic aspects of Pantepui are presented.

Additional key words: Pantepui, Guiana Highlands, biogeography.

Recent expeditions to several table-top mountains and other elevated ridges of the Guiana Highlands, also known as "Pantepui" (Mayr & Phelps 1967), have yielded new taxa of Lepidoptera (e.g., Viloria 1994, Viloria & Pyrcz 1994). In this paper we describe a new hawk moth from a mountain system in extreme southern Venezuela. In contrast to most of the other 100 or so species and subspecies currently placed in the American genus *Xylophanes* Hübner (Rothschild & Jordan 1903, D'Abrera 1987), the new subspecies appears to have an extremely limited range, being confined to Mt. Neblina and Mt. Aracamuni, two neighboring mountains at the southern edge of Pantepui. Here the new taxon replaces the nominate form, which is common and widespread in the surrounding lowlands. Additional new taxa can be expected to occur in other as yet unexplored mountainous areas of this region. Indeed, one new species of *Xylophanes* already has been found in the mountains of Jaua-Sarisariñama, a highland complex about 400 km northeast of the Neblina-Aracamuni system (unpubl. data of the authors). A checklist of all sphingid species so far found in the Venezuelan State of Amazonas (including Pantepui) will be presented elsewhere.

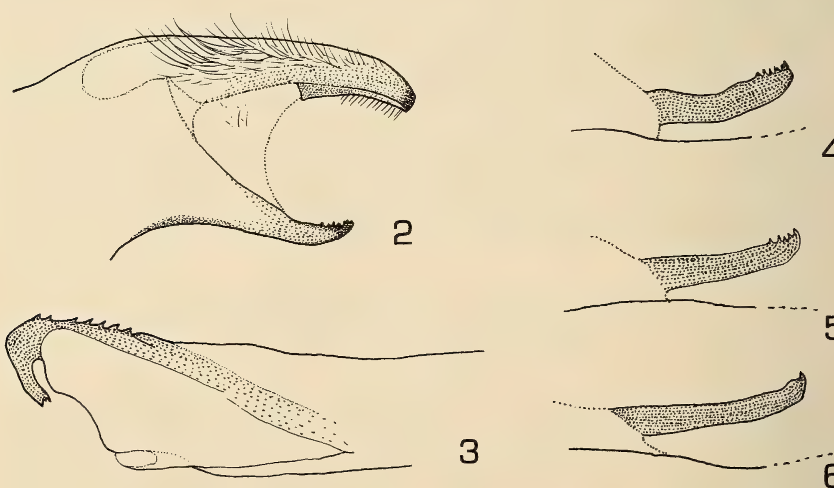
Xylophanes tersa chaconi **De Marmels, Clavijo & Chacin, new subspecies**
(Figs. 1–7)

Diagnosis. Male general coloration dark ash-brown; head and thorax dark chestnut between the dingy white lateral bands. Base of hindwing dark brown to black, extending distally along veins, intersecting postmedian row of diffuse, ash-brown spots. Underside of wings dark ash-brown, usually with ferruginous or brown postmedian areas of variable extension. *X. tersa chaconi* is similar in color pattern to an as yet undescribed species from the mountains of Jaua-Sarisariñama. These two taxa may be separated by development and coloration of the pale postmedian dorsal hindwing spots: in the undescribed species from Jaua-Sarisariñama these spots are clear-cut and cream-colored, while in *X. tersa cha-*

FIG. 1. Male holotype of *Xylophanes tersa chaconi*. Dorsal surface on right, ventral on left.

coni they are not sharply defined and ash-brown. The uncus is smooth ventrally in the Jaua-Sarisariñama species, but has a more or less triangular process at the end of the anal membrane in both *X. tersa chaconi* and *X. tersa tersa*. The aedeagus is considerably more chitinized in the Jaua-Sarisariñama species than in *X. tersa chaconi*.

Description. *Male. Dorsal surface* (Fig. 1): head and thorax dark chestnut between sharply defined, dingy white lateral bands, the latter paler on tegulae; antenna dingy white; forewing with series of dark, oblique, parallel lines running from anal margin towards tip;



FIGS. 2–6. Male genitalia of *Xylophanes tersa chaconi*. **2**, uncus and gnathos. **3**, aedeagus. **4**, right harpe of a paratype from Mt. Aracamuni (south). **5**, same of a paratype from Mt. Neblina. **6**, same of another paratype from Mt. Neblina. Figs. 2, 5–6 in left lateral view.

FIG. 7. Venezuela, showing known localities of *X. tersa chaconi*. 1 is Mt. Aracamuni (type locality), 2 is Mt. Neblina.

fringe ash brown; base of hindwing dark brown to black, extending distally along veins across postmedian row of diffuse, ash-brown spots, connecting with ash-brown submarginal area; apical area same color; fringe paler than in forewing, cream-colored; abdomen ash-brown with five ill-defined dark longitudinal lines. *Ventral surface* (Fig. 1): first and second segment of palpus pale ferruginous; thorax without collar, ferruginous laterally between wing bases and coxae; forewing ash-brown with an oblique row of minute dark postmedian spots within ferruginous (or brown) postmedian area, or these spots almost absent; hindwing similar, a series of three to four dark parallel stripes running from anal field towards costal margin; outer stripe preceding zigzagging submarginal band, dissolving into row of small spots; entire pattern frequently blurred basally; tibiae grey with dingy white dorsal line; first segment of fore tarsus with external row of small spines; smaller apical spur of hind tibia less than half the length of large spur; abdomen ash-brown with variable amount of ferruginous laterally. *Genitalia* (Figs. 2–6): uncus ventrally with triangular postmedian salient; gnathos chitinized and serrate dorsally in distal portion; aedeagus not strongly chitinized; harpe slightly bulbous subapically and serrate dorsally near tip (slender and parallel-sided in specimens from Mt. Neblina); in one specimen from Mt. Neblina the harpe lacks serrations and terminates in a hook. *Size.* Length from head to tip of abdomen 40–45 mm; fore wing 31.6–35.5 mm; antenna 15–18 mm. *Female and early stages*: unknown.

Types. *Holotype.* Male: VENEZUELA, State of Amazonas, Serranía de La Neblina National Park, Mt. Aracamuni (South), 01°26'N, 65°47'W, 1550 m, 30 Oct.–3 Nov. 1987,

Expedition "Fundación Terramar" (A. Chacón and E. Osuna). *Paratypes*: 9 males, same locality data as holotype; 3 males, Mt. Aracamuni (North), 01°32'N, 65°49'W, 1415 m, 24–30 Oct. 1987, same collectors; 2 males, Mt. Neblina, Camp X, 00°54'N, 60°02'W, 1690 m, 12 Feb. 1985, Expedition "Fudeci" (W. E. Steiner); 1 male, Camp XI, 00°52'N, 65°58'W, 1450 m, 25–28 Feb. 1985, Expedition "Fudeci" (P. J. & P. M. Spangler and R. A. Faitoute); all specimens deposited in Museo del Instituto de Zoología Agrícola (MIZA), Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela.

Etymology. The new taxon is named in honor of Mr. Aníbal Chacón, technical assistant and staff member of the MIZA. He is the collector of most of the specimens.

Habitat. The specimens from Mt. Neblina, taken by W. E. Steiner, were collected at "black light in mixed scrub forest near stream and canyon rim" (collector's label); those from Mt. Aracamuni in an identical type of habitat (A. Chacón pers. comm.).

DISCUSSION

Xylophanes tersa tersa occurs from Canada to Argentina. The adults exhibit little individual and no definite geographical variation either in hindwing maculation or forewing ground color (Rothschild & Jordan 1903, Hodges 1971). No subspecies of *X. tersa* has so far been described from continental America. Subspecies *X. t. cubensis* Gehlen, from Cuba, differs little from the nominate form. The name *tristis* Closs refers to "an insignificantly darkened form" of *tersa* (Draudt 1939:893).

The Venezuelan specimens closely resemble an example from Florida, USA, figured in Hodges (1971:plate 13, fig. 18), except, perhaps, for the slightly more olivaceous tint of the thoracic dorsum in most Venezuelan specimens, which appears to be chestnut in the figured individual from the USA. However, color differences between *X. tersa tersa* and *X. tersa chaconi* are striking. Allopatry (to parapatry) seems to prevent the two populations from intergrading, and our assigning subspecific rank to *X. t. chaconi* is therefore provisional, following the view that the absence of genitalic differences does not warrant higher rank.

A similar case in dragonflies (Odonata) of a widespread lowland species with an "aberrant" population of probable subspecific status on some Pantepui mountains was recorded by De Marmels (1994). In this case, however, some apparent intergradation in the tepuyan population can be observed, probably due to occasional vagrants from the lowland (but not vice versa). In addition, Mayr & Phelps (1967) list 18 bird species that are widespread in the tropical lowlands, including the proper foot of Pantepui, having endemic subspecies in Pantepui.

The biogeography of Pantepui is usually misunderstood. The presence in Pantepui of animal and plant taxa with, for example, Andean affinity, is persistently explained by "hill-hopping," "small-scale long distance dispersal," "propagules," "colonization flights," or "jumps," from the Andes to Pantepui (e.g., Mayr & Phelps 1967, Viloria & Pyrcz 1994, and references therein). Dispersal origins seem improbable, as the Andes are much younger geologically (their uplifting began in the Eocene, see Schubert & Huber 1989) than Pantepui. Moreover, the fact that the

primitive forms are presently found in Pantepui while the derived taxa thrive in the Andes indicates that the latter probably did not migrate from the Andes to Pantepui (see Viloria & Pyrcz 1994).

The pantepuyan fauna likely originated *in situ* from ancestral forms, some of which populated vast areas of the Guiana shield and part of the sedimentary basins to the north and west, regions which later were "captured" by the uplifting of the Andes (e.g., the "yungas" of Bolivia). Their descendants in the Andes and in Pantepui became disjunct as a consequence of extinction in the intervening lowlands, eventually yielding new taxa (Croizat 1958, 1964, 1976, Heads 1985).

In apparent contrast to birds and butterflies, the pantepuyan damselflies (Odonata, Zygoptera) contain extant taxa that are true relicts of ancient (Mesozoic) origin. The monobasic genus *Rimanella* (Needham) (Amphipterygidae), endemic to Pantepui, lacks South American relatives, being closely related only to *Pentaphlebia* Förster of the highlands on the Nigeria/Cameroon border, not to the only other American amphipterygid genus, *Amphipteryx* Selys, of Central America and Mexico (Lieftinck 1971, Novelo Gutierrez 1995, de Marmels pers. obs.). *Amphipteryx* has obvious affinities (through a "transpacific track," Croizat 1958) with the southeast Asian genus *Devadatta* Kirby. Similarly, the endemic pantepuyan calopterygine genus *Iridictyon* Needham & Fisher is not closely related to the North American Calopteryginae (a subfamily otherwise absent from Central and South America), but to African *Phaon* Selys, and *Umma* Kirby (Needham & Fisher 1940, Fraser 1957) and, probably, to the South Asian *Vestalis* Selys. Such evidence is inconsistent with origin by disperal. More probably, a common ancestor of *Rimanella* + *Pentaphlebia* was already distributed over parts of the African and Guiana shields when Africa and South America and, consequently, the two ancient shields were still linked together in the Jurassic. In the early Cretaceous the ancestral population became split by the opening of the Atlantic Ocean. The ancient dispersal of the common ancestor is manifested by the "transatlantic track," which is not a migration route but a line still tying together the fragments of the once compact area of ancestral distribution (Croizat, 1958, 1964).

It is interesting to note that in 1988 a large swarm of African migratory locusts (*Schistocerca gregaria* Forskal) did in fact cross the Atlantic by flight, probably favored by special meteorological circumstances, and reached several Caribbean islands as well as the whole caribbean coast of Venezuela and Suriname (Cerdá 1989, Ritchie & Pedgley 1989, Stemshorn 1989). However, the species failed to establish itself and soon vanished, despite the existence of potentially suitable tropical desert habitat along the northern coast of Venezuela. Lastly, we wish to emphasize the parallel between the situation described here for *Xylo-*

phanes and that of *Pedaliodes* Butler (Satyridae) in the same geographic area (see Viloria & Pircz 1994). These pronopholine butterflies are sedentary and have low vagility, and the observed endemism and vicariance among their taxa, and their apparent inability even to colonize neighboring mountains within the Andes, renders them equally unlikely candidates for long-distance colonization flights between the Andes and Pantepui, both in the past and the present.

ACKNOWLEDGMENTS

We are indebted to W. E. Steiner, P. J. & P. M. Spangler, and R. A. Faitoute (all of the Smithsonian Institution, USA) for depositing the specimens collected by them on Mt. Neblina in MIZA. Fundacion TERRAMAR and FUDECI (both Caracas) organized the expeditions, and Fundación Polar (Caracas) and Fundacite Aragua gave financial support.

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NEW SPECIES OF *ACTINOTE* HÜBNER (NYMPHALIDAE: ACRAEINAE) FROM SOUTHEASTERN BRAZIL

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ABSTRACT. Three new species of *Actinote* (Acraeinae) from southeastern and southern Brazil are described: ***Actinote dalmeidai***, ***A. catarina*** and ***A. bonita***. Diagnoses and illustrations are provided for the new species and for the previously described *A. alalia*, *A. conspicua*, *A. surima*, and *A. quadra*.

Additional key words. *Actinote dalmeidai*, *A. catarina*, *A. bonita*, mimicry.

Butterflies of the genus *Actinote* Hübner (Acraeinae) are well known for their involvement in Müllerian mimicry complexes (Brown & Benson 1974, Francini 1989, Brown & Francini 1990) and for their intraspecific variation in wing coloration and pattern. These two features account for the large number of varieties, subspecies, and species that have been described since the beginning of this century.

The species described herein belong to the "orangish red mimicry complex" of Francini (1989) and the "*alalia* mimicry complex" of Brown and Francini (1990), both of which include the deep orange colored *Actinote alalia* (Felder), *A. conspicua* (Jordan), and *A. surima* Schaus. Species in this mimicry complex are generally univoltine, the adults flying during the wet season. They are restricted to forested areas in which the humidity is high all year long. In latitudes south of 23°S, they are found only at elevations above 1000 m.

Species in this mimicry complex are characterized by a dark orange and brown striped pattern, and a hindwing upper surface with a dark brown margin from the costal to the anal area, the width of which is diagnostic for the species. The pattern observed in the under surface of the hindwing, although variable, is one of the most useful diagnostic features for the species. Herein we present descriptions of three new cryptic species of *Actinote* in the "orangish red" complex, commonly misidentified as *Actinote alalia* (Felder). Diagnoses, illustrations of male and female genitalia, synonymies, and observations on the natural history of previously described orange-colored species of *Actinote* also are provided.

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MATERIALS AND METHODS

The specimens studied are deposited in the following institutions: Department of Zoology, Universidade Federal do Paraná, Curitiba PR Brazil (DZ); Museu Anchieta, Porto Alegre RS Brazil (MAPA). Adults and immatures from two private collections also were studied: Olaf H. H. Mielke (OM, at Universidade Federal do Paraná), and R. B. Francini (RBF, now incorporated into the collection of Museu de Zoologia USP). Dissections were performed after treatment with 10% KOH. Dissected parts were kept in a solution of glycerin and 70% ethanol, and are deposited in the collections along with adult specimens. The presence of pyrrolizidine alkaloids and cyanogenic glycosides was detected using the techniques described in Francini (1989) and Brown and Francini (1990).

***Actinote dalmeidai* Francini, new species**
(Figs. 1a, 2a–d, 3a)

Actinote alalia D'Almeida 1935a:71, 93; Brown 1987:41; Brown 1988:36; Francini 1989:41.
Actinote sp. close to *alalia*, Brown 1992:158.

Diagnosis. *Actinote dalmeidai* can be distinguished from other species by the following features: forewing upper surface orange stripe number 1 and spot number 2 rarely fused. Hindwing under surface whitish yellow, normally with a dark brownish orange area present distal to V-shaped mark, variable in size. In males, last tergum of abdomen short, truncate. Valvae relatively thin and bowed, apex rounded. Of all orange species present in Southeastern Brazil, the wing pattern of *A. dalmedai* is most similar to that of *A. alalia*.

Description. *Male* (Fig. 1a): forewing length 23 to 34 mm; holotype 29 mm. Forewing upper surface with orange stripes and spots normally clearly separated by brown scales, orange stripe number 1 and spot number 2 rarely fused. Hindwing upper surface with same color pattern as forewing, with variable V-shaped mark. Hindwing under surface whitish yellow, somewhat "smoky;" a brownish orange area (darker than upper surface) normally present distal to V-shaped mark, more faint towards margin, from nearly absent to almost covering entire under surface of the wing, both distal and caudal of the V-shaped mark; dark margin extended from costal to anal areas visible on under surface. In males, last tergum of abdomen short, truncate. *Male genitalia* (Fig. 2a–d): valvae relatively thin and bowed, apex rounded. Shape of the uncus+tegumen, juxta and aedeagus variable. *Female*: as described for male, but upper and under surfaces of the wings paler. *Female genitalia:* sterigma small, sculptured (Fig. 3a).

Distribution. Southeastern Brazilian highlands, known from the states of Rio de Janeiro, Minas Gerais, São Paulo, Paraná; few specimens known from the states of Santa Catarina and Rio Grande do Sul.

Types. Holotype male: BRAZIL: Paraná, São José dos Pinhais, 850m, 26.XI.1978 (O. H. Mielke) (DZ 3734). Paratypes: BRAZIL: 10♂ Rio de Janeiro, Mauá, Itatiaia 1200m XII.1957 (DZ 3126, 3717–21, 3743–44, 3754, 3758); 2♂ Rio de Janeiro, Resende, Itatiaia, 1200m, 10.I.1973 (DZ 3712–13); 1♂ Rio de Janeiro Itatiaia, Nordostseite, 1300m, XII.1957 (DZ 3722); 2♂ Rio de Janeiro, Itatiaia, Südseite, 1100m, 4.XII.1963 (DZ 3715–16); 1♂ Rio de Janeiro, Itatiaia, Südseite, 800m, 12.I.1969 (DZ 3714); 1♂ Minas Gerais, Juiz de Fora, 500–800m, 17.XI.1953 (DZ 3476); 1♂ Minas Gerais, Poços de Caldas, 1250m, 24.12.1966 (DZ 3723); 1♂ São Paulo, Eug. Lefévre, Campos do Jordão, 1200m, 2.XII.1937 (DZ 3710); 1♂ São Paulo, Eug. Lefévre, Campos do Jordão, 1200m, 17.XII.1952 (DZ 3711); 1♂ São Paulo, Eug. Lefévre, Campos do Jordão, 1200m, 8.XII.1957 (DZ 3733); 1♂ São Paulo, Boracéa, Salesópolis, 13.XII.1941 (DZ 3724); 9♂ Paraná, Curitiba, 10.XII.1969 (DZ 3124, 3145, 3140, 3117, 3748–52), 2♂ Paraná, Curitiba, 13.XII.1968 (DZ 3753, 3756); 1♂ Paraná, Curitiba, 20.III.1988 (DZ 3742); 1♂ Paraná, Piraquara, 13.XII.1969 (DZ 3747); 1♂ Paraná,

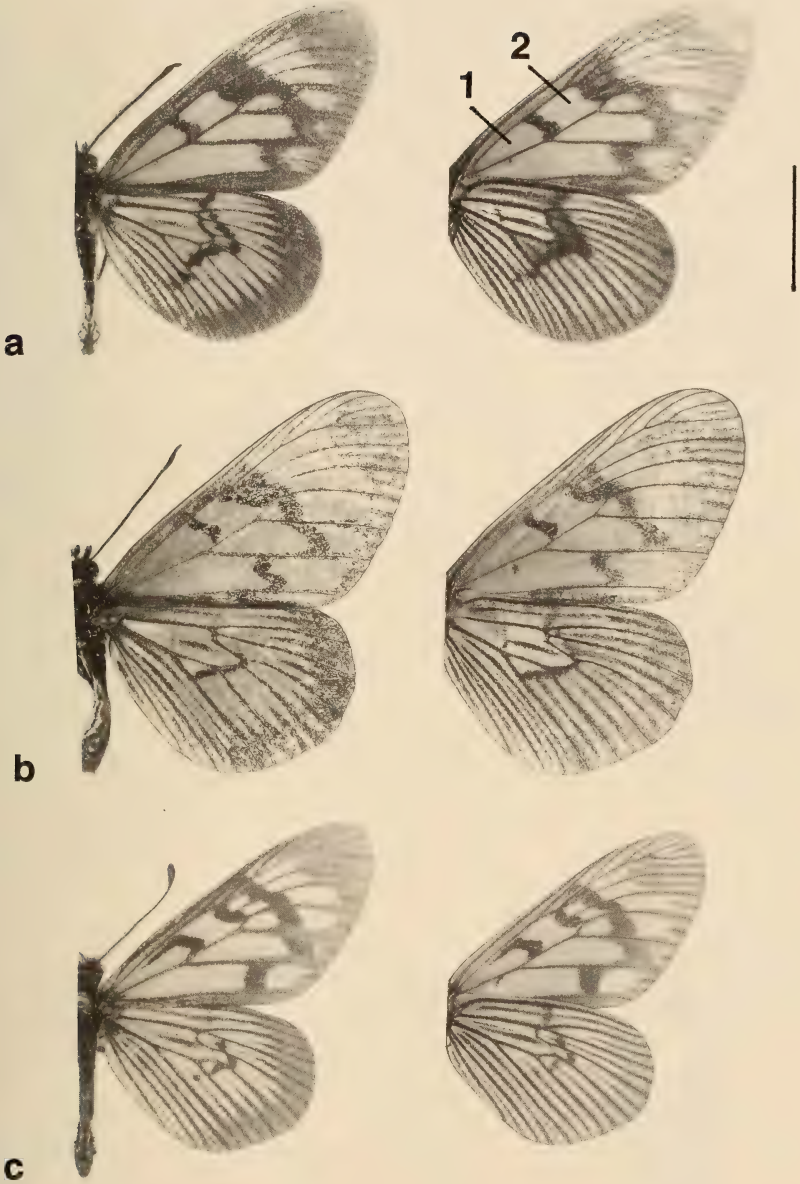
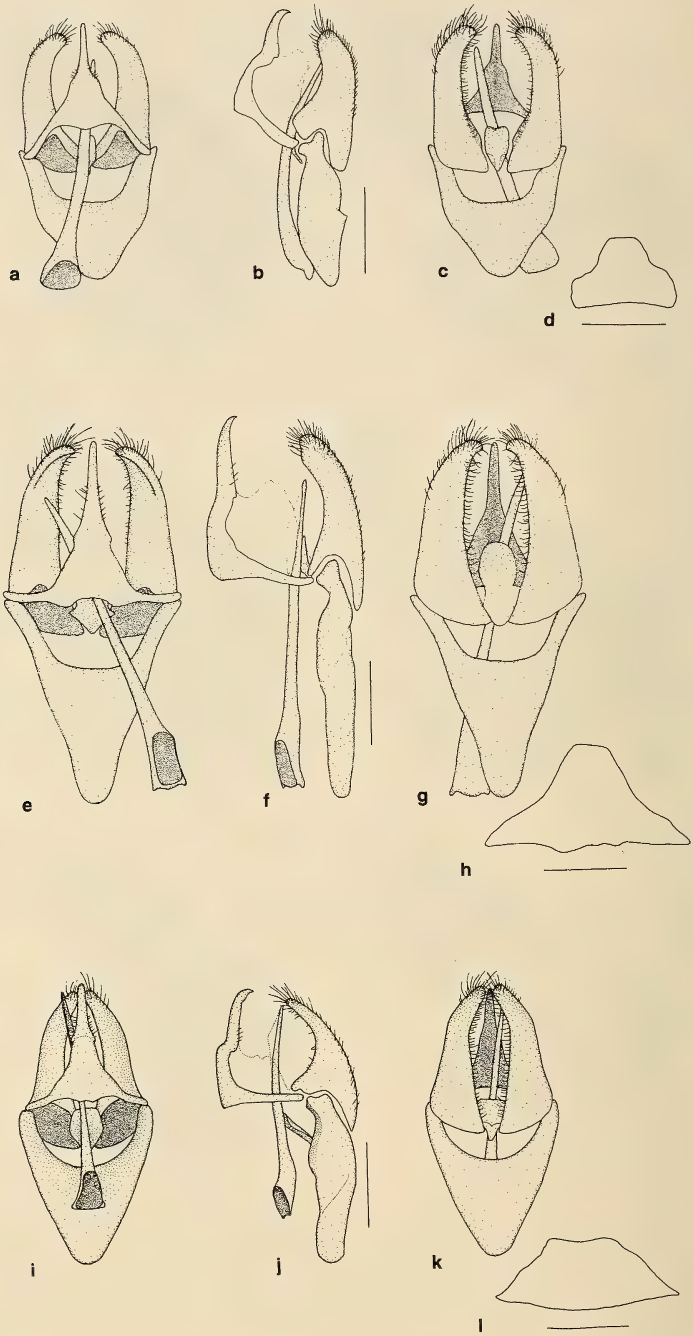


FIG. 1. Upper and under surfaces (left and right respectively) of three new species of *Actinote*. (a) *A. dalmeidai* Francini, new species. Holotype ♂ DZ 3734, forewing length 29 mm. See text for explanation on stripe number 1 and spot number 2; (b) *A. catarina* Penz, new species. Holotype ♂ DZ 3139, forewing length 30 mm; (c) *A. bonita* Penz, new species. Holotype ♂ DZ 3761, forewing length 27 mm. Scale bar: 10 mm.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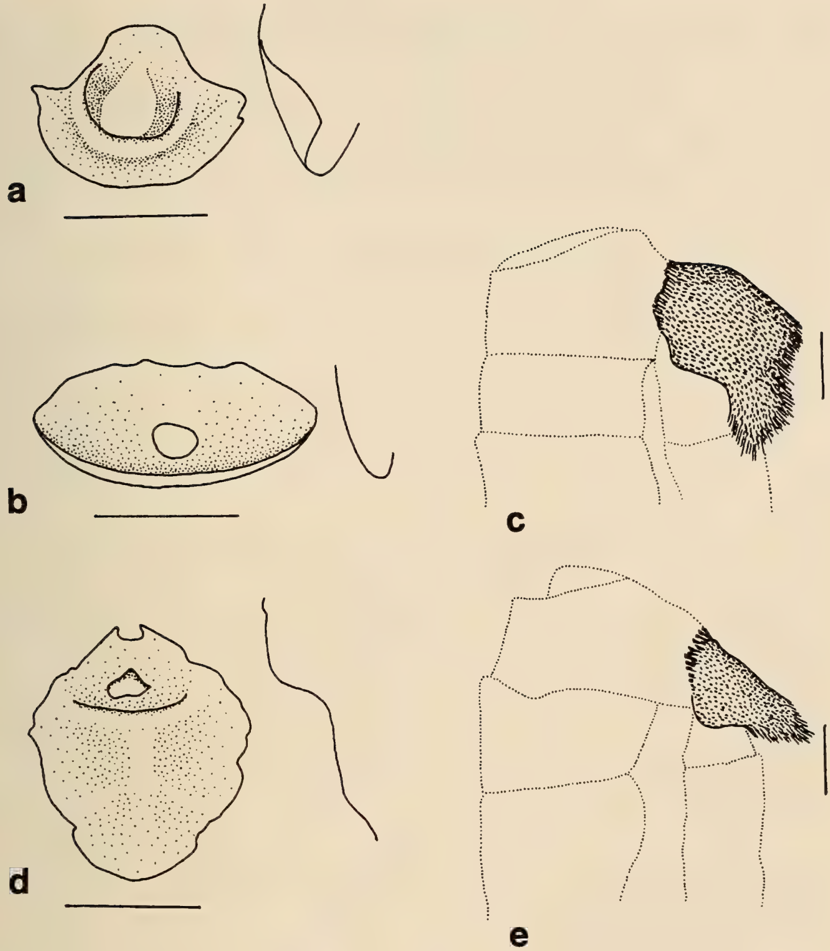

FIG. 3. Female genitalia of three new species of *Actinote*; the line to the left of the figure schematically represents the cross section. *Actinote dalmeidai* Francini, new species. Female genitalia RBF collection: (a) sterigma. *Actinote catarina* Penz, new species. Female genitalia MAPA collection: (b) sterigma; (c) sphragis. *Actinote bonita* Penz, new species. Female genitalia DZ collection: (d) sterigma; (e) sphragis. Scale bar: 1 mm.

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FIG. 2. Male genitalia of three new species of *Actinote*. *Actinote dalmeidai* Francini, new species. Male genitalia DZ 3126: (a) dorsal view, (b) lateral view, (c) ventral view; RBF L659#52: (d) 8th sternum. *Actinote catarina* Penz, new species. Male genitalia MAPA 6011: (e) dorsal view, (f) lateral view, (g) ventral view; DZ 3150: (h) 8th sternum. *Actinote bonita* Penz, new species. Male genitalia DZ 3118: (i) dorsal view, (j) lateral view, (k) ventral view, (l) 8th sternum. Scale bar: 1 mm.

São José dos Pinhais, 850m, 14.XII.1966 (DZ 3746); 1♂ Paraná, São José dos Pinhais, 850m, 17.XII.1966 (DZ 3745); 13♂ Paraná, São José dos Pinhais, 850m, 26.XII.1978 (DZ 3141–42, 3149, 3159, 3313, 3730–32, 3735, 3741, 3755, 3757); 15♂ Paraná, São José dos Pinhais, 850m, 15.XII.1979 (DZ 3114, 3143–44, 3146, 3154–55, 3433, 3475, 3728–29, 3736–40); 1♂ Paraná no date (DZ 3709); 3o Santa Catarina, São Bento do Sul, 850m, 2.XII.1969 (DZ 3122, 3725, 3727; 1♂ Santa Catarina, São Bento do Sul, 850m, 3.XII.1969 (DZ 3726); 1♂ Rio Grande do Sul, Cambará do Sul, Itaimbezinho, 2.I.1981 (DZ 3113). Holotype and paratypes at the Department of Zoology, Universidade Federal do Paraná, Brazil (DZ).

Etymology. The species is named after Romualdo Ferreira D'Almeida (1891–1969). We acknowledge the work of this passionate lepidopterist, who took the first steps toward the better understanding of the taxonomy of *Actinote* in Brazil.

Biology. HOSTPLANTS: *Eupatorium punctulatum*, *Eupatorium* sp. (R.B.F. pers. obs.). IMMATURES: eggs of *A. dalmeidai* are barrel-shaped, yellow when freshly laid, pale salmon when mature; micropyle depression present; deposited in dense clusters of 200–300, packed together very closely. Mature larva with background coloration bluish green; head green; scoli short. Pupa white with black markings, 5 pairs of dorsal spines. TOXICITY: pyrrolizidine alkaloids were detected in the adults; strong cyanogenesis is present in all stages (Brown & Francini 1990). MIMICRY: *Actinote dalmeidai* was included in the "orangish red mimicry complex" of Francini (1989) and "*alalia* mimicry complex" of Brown and Francini (1990).

Actinote catarina Penz, new species
(Figs. 1b, 2e–h, 3b–c)

Diagnosis. *Actinote catarina* can be distinguished from other species by the following features: forewing orange stripe number 1 and spot number 2 frequently fused; other spots also commonly fused. Hindwing under surface colored area generally same orange shade as upper surface background, distal to the V-shaped mark, variable from absent or pale to large and bright covering more than half of the under surface. In males, last tergum of the abdomen long, pointed. Valvae relatively broad, apex pointed. As cmpard to the other orange species present in Southeastern Brazil, the wing pattern of *A. catarina* can be considered intermediate between those of *A. conspicua* and *A. alalia*.

Description. *Male* (Fig. 1b): forewing length 27 to 31 mm; holotype 30 mm. Forewing upper surface with well developed orange stripes and spots, orange stripe number 1 and spot number 2 frequently fused; other spots also commonly fused. Hindwing upper surface with same color pattern as forewing, with variable V-shaped mark. Hindwing under surface whitish yellow; orange colored area (generally same color as upper surface) located distal to the V-shaped mark varies from absent or pale to large and bright covering more than half of the under surface; dark margin extended from costal to anal areas visible on under surface. In males, last tergum of abdomen long, pointed. *Male genitalia* (Fig. 2e–h): valvae reasonably broad, apex pointed. Shape of uncus+tegumen, juxta and aedeagus variable. *Female*: as described for male, but upper and under surfaces of wings paler; forewing discal cell and anal region moderately transparent. *Female genitalia* (Figs. 3b–c): sterigma broad; sphragis broad and horizontally attached to the abdomen.

Distribution. Southern Brazilian highlands, known from the states of Paraná, Santa Catarina and Rio Grande do Sul.

Types. Holotype male: BRAZIL: Santa Catarina, Santa Cecília, 1000m, 22.II.1973 (O. H.Mielke) (DZ 3139). Paratypes: BRAZIL: 1♂ Paraná, São José dos Pinhais (DZ 3707); 1♂ Santa Catarina, Curitibanos, 1050m, 24.II.1973 (DZ 3470); 1♂ Santa Catarina, Praia Grande Faxinal, 1.I.1984 (MAPA 6828); 1♂ Santa Catarina, Lages, P.N. Pedras Brancas, 920m, 13.II.1973 (DZ 3706); 1♂ Santa Catarina, Rio das Antas, II.1953 (DZ 3705); 2♂ Santa Catarina, Santa Cecília, 1200m, 22.II.1973 (DZ 3150, 3704); 1♂ Rio Grande do Sul, Aparados da Serra, I.1985 (MAPA 6829); 1♂ Rio Grande do Sul, Panambi IV.1973 (DZ 3151); 1♂ Rio Grande do Sul, Rio Guarita XII.1962 (DZ 3703); 1♀ Rio Grande do Sul, São Francisco de Paula, Itaimbezinho 25.I.1959 (MAPA 6615); 1♀ Rio Grande do Sul, São Francisco de Paula 23.I.1959 (MAPA 6612); 2♀ Rio Grande do Sul, São Francisco de

Paula, RS no date (DZ 3702, 3708). Holotype and paratypes at the Department of Zoology, Universidade Federal do Paraná, Brazil (DZ), paratypes at Museu Anchieta, Porto Alegre, Brazil (MAPA).

Etymology. The species is named after Santa Catarina state; *A. catarina* is restricted in range to southern states in Brazil.

Biology. HOSTPLANTS: unknown. IMMATURES: unknown. TOXICITY: unknown. MIMICRY: *Actinote catarina* species fits the attributes of the "orangish red mimicry complex" of Francini (1989) and "*alalia* mimicry complex" of Brown and Francini (1990), and should be considered part of this complex hereafter.

Actinote bonita Penz, new species
(Figs. 1c, 2i–l, 3d–e)

Diagnosis. *Actinote bonita* can be distinguished from other species by the following features: orange stripes and spots never fused on forewing upper surface. Hindwing under surface whitish yellow, pale and homogeneous, lacking dark brown marginal shading. In males, last tergum medium sized. Valvae wide at base, thin from middle portion to apex. Of all orange species present in Southeastern Brazil, the wing pattern of *A. bonita* is most similar to that of *A. quadra*.

Description. *Male* (Fig. 1c): forewing length 25 to 27 mm; holotype 27 mm. Forewing upper surface with orange stripes and spots widely separated by brown scales. Hindwing upper surface with same color pattern as forewing, with thin V-shaped mark; dark margin extended from costal to anal areas slightly diffuse. Hindwing under surface whitish yellow, pale and homogeneous; dark brown margin absent, dark-colored scales restricted to wing veins. Last tergum medium sized. *Male genitalia* (Fig. 2i-l): valvae wide at base, thin from middle portion to apex. Aedeagus thin. Shape of the uncus+tegumen, juxta and aedeagus variable. *Female*: as described for male, but upper and under surfaces of wings paler. *Female genitalia* (Fig. 3d-e): sterigma longer than broad, mildly sculptured; sphragis delicate.

Distribution. Southeastern Brazilian highlands, known from the states of Minas Gerais and São Paulo.

Types. Holotype male: BRAZIL: Minas Gerais, Monteverde, Camanducaia, 1650m, 23.XII.1968 (DZ 3761). Paratypes: BRAZIL: 3♂ Minas Gerais, Monteverde, Camanducaia, 1650m 23.XII.1968 (DZ 3118, 3759–60). Holotype and paratypes at the Universidade Federal do Paraná (DZ).

Etymology. The species is named after "Bonita," a song by Tom Jobim.

Biology. HOSTPLANTS: *Eupatorium inulaefolium* (R.B.F. pers.obs.). IMMATURES: eggs of *Actinote bonita* are barrel-shaped, yellow when freshly laid, faint salmon when mature; micropyle depression absent; deposited in clusters of 200–400, density of cluster intermediate between *A. dalmeidai* and *A. conspicua*. Mature larva with background coloration bluish black; head black; thoracic segments completely black laterally and ventrally; scoli short. Pupa white with black markings, 5 pairs of dorsal spines. TOXICITY: cyanogenesis was detected in all stages (R.B.F. pers.obs.).

OTHER ORANGE-COLORED SPECIES OF ACTINOTE

Actinote alalia (Felder)
(Fig. 4a–c)

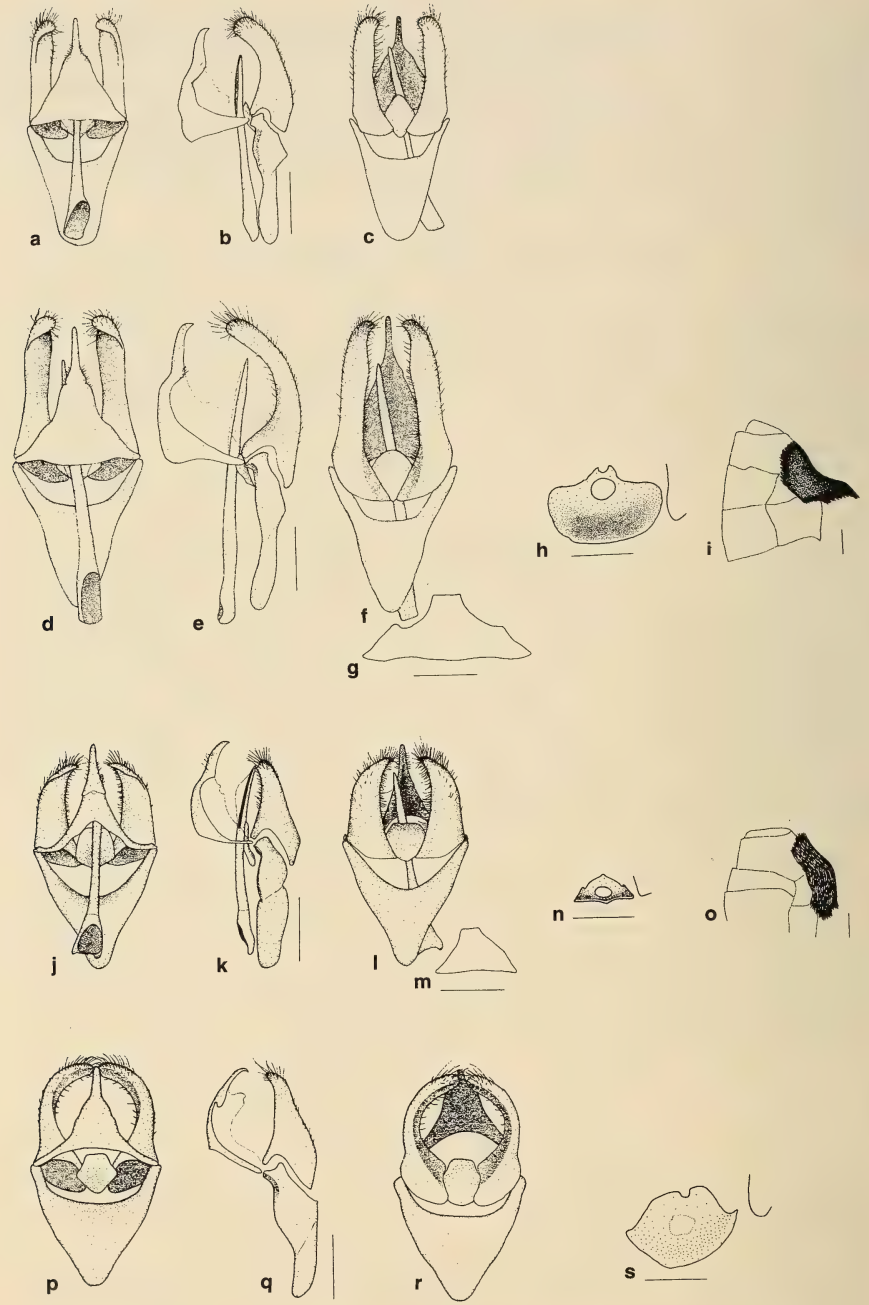
Acraea alalia Felder 1860:105; Kirby 1871–77:136; Jones 1883:36; Jones 1883:8; Fritz Müller 1883:216; Mabille 1896:64.

Acraea eulalia Fritz Müller 1878:296.

Actinote alalia s. *alalia* Eltringham and Jordan 1913:10; Jordan 1913b:374.

Actinote alalia Jordan and Eltringham 1916:19; D'Almeida 1935a:93; Ebert 1969:35; Lewis 1975:43, 227; Smart 1976:265; D'Abrera 1987:445; Ackery 1988:136; Francini 1992:16 fig.6–14 [ALA].

Acraea (Actinote) alalia Pierre 1987:22.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Diagnosis. Intermediate in size, males 28 to 31 mm (DZ collection). Hindwing under surface greyish yellow; deep orange or, less frequently, brownish orange colored area distal to the V-shaped mark, variable in size. Male genitalia (Fig. 4a–c): valvae neither broad nor thin, apex round.

Biology. HOSTPLANTS: *Eupatorium intermedium* and *Eupatorium* sp. aff. *E. intermedium* (R.B.F. pers. obs.). IMMATURES: eggs of *Actinote alalia* are barrel-shaped, yellow when freshly laid, burgundy when mature; micropile depression absent; deposited in clusters of 200–400, cluster density similar to *A. bonita* clusters. Mature larva with background coloration pinkish brown, head black; scoli very short. Pupa dark orange with black markings, 5 pairs of dorsal spines. TOXICITY: pyrrolizidine alkaloids were detected in the adults; strong cyanogenesis in all stages (Brown and Francini 1990). MIMICRY: this species is included in the "*alalia* complex" of Brown and Francini (1990).

Actinote conspicua (Jordan)
(Fig. 4d–i)

Actinote alalia conspicua Jordan 1913a:32; Jordan 1913b:374 pl. 82e; Eltringham and Jordan 1913:10; Jordan and Eltringham 1916:18; Brown and Mielke 1968:151; D'Abrera 1987:445.

Actinote conspicua Ebert 1969:35; Francini 1992:16 fig.6–14 [CON].

Diagnosis. Generally large, males 24 to 38 mm (DZ collection). Orange spots and stripes on upper surface of both wings deep colored. Hindwing under surface deep orange (but one specimen found (DZ) with the underside of the hindwing yellowish colored, maybe still teneral when collected). Hindwing dark brown margin markedly broad, both on upper and under surfaces. *Male genitalia* (Fig. 4d–g): valvae long and thin, bowed dorsoventrally. This species has the deepest coloration among members of its mimicry complex. Females larger than males, only slightly paler than males. *Female genitalia* (Fig. 4h–i).

Biology. HOSTPLANTS: *Mikania hirsutissima* (R.B.F. pers.obs.). IMMATURES: presently under study by R.B.F. TOXICITY: cyanogenesis was detected in eggs and first instar larvae (R.B.F. pers.obs.). MIMCRY: this species was included in the "orangish red mimicry complex" of Francini (1989) and "*alalia* mimicry complex" of Brown and Francini (1990).

Actinote surima Schaus
(Fig. 4j–o)

Actinote surima Schaus 1902:392; Jordan 1913b:374 pl. 82 f,g; Eltringham and Jordan 1913:13; Jordan and Eltringham 1916:19 Figs. 8, 9; Hayward 1931:29,139 pl. 8; Monte 1934:199; Hayward 1935:97; D'Almeida 1935a:94; D'Almeida 1935b:488; Schweizer and Webster-Kay 1941:14; Biezanko and Pitton 1941:9; Hayward 1950:209; Biezanko, Rufinelli and Carbonell 1957:127; Brown and Mielke 1967:151; D'Araujo e Silva et al. 1968:340; Ebert 1969:35; Brown and Benson 1974:218 pl. 5 fig.1; Smart 1976:191, 265 pl. 5 fig.1; Brown 1984:158; Almeida, Souza and Marques 1986:33; D'Abrera 1987:445; Francini 1989:44 and several other pages, several figs; Brown 1988:36; Francini 1992:26 fig.6–14 [SUR].

←

FIG. 4. Male and female genitalia of orange-colored species of *Actinote*. *Actinote alalia* (Felder). Male genitalia DZ 2974: (a) dorsal view, (b) lateral view, (c) ventral view. *Actinote conspicua* (Jordan). Male genitalia DZ 3130: (d) dorsal view, (e) lateral view, (f) ventral view, (g) 8th sternum. Female genitalia DZ collection: (h) sterigma, (i) sphragis. *Actinote surima* Schaus. Male genitalia MAPA 6687: (j) dorsal view, (k) lateral view, (l) ventral view; RBF L643#11: (m) 8th sternum. Female genitalia RBF L643F10069#25: (n) sterigma; MAPA 6700: (o) sphragis. *Actinote quadra* Schaus. Male genitalia DZ 2970: (p) dorsal view, (q) lateral view, (r) ventral view. Female genitalia OM 6655, drawn from pinned specimen (s) sterigma. Scale bar: 1 mm.

Actinote surima forma *punctata* Hayward 1935:97 pl. 11 fig. 61; Hayward 1950:209.
Acraea (Actinote) surima Pierre 1987:22.

Diagnosis. Small, male and female specimens 20 to 30 mm (RBF and MAPA collections). Orange color slightly lighter than in other species of same mimicry complex. Hindwing under surface yellowish, with same pattern as upper surface; V-shaped mark always well developed in both upper and under surfaces. *Male genitalia* (Fig. 4j–m): valvae broad and short, pointed apex. *Female genitalia* (Fig. 4n–o).

Biology. HOSTPLANTS: *Eupatorium intermedium*, *Senecio brasiliensis* (Francini 1989; Brown & Francini 1990); *Mikania hirsutissima*, *Symphiopappus reticulatus* (Francini 1989); *Eupatorium buniifolium* (Biezanko et al. 1974); *Symphiopappus casaretoi* (C.M.P. pers.obs.). Biezanko et al. (1974) also list *Amaranthus hybridus* as a host plant for this species; because *Actinote* larvae fall from the host when disturbed and frequently wander off the plant for pupation, we regard this record to be inaccurate. IMMATURES: eggs of *Actinote surima* are barrel-shaped, yellow when freshly laid, burgundy when mature; micropyle depression absent; deposited in clusters of 200–400, of density similar to *A. bonita* and *A. alalia* clusters. Mature larva polymorphic: background coloration varies from yellowish pink to bluish black, head black; scoli short. Pupa white with black markings, 5 pairs of dorsal spines. TOXICITY: pyrrolizidine alkaloids were detected in all stages; strong cyanogenesis was detected in all stages (Brown and Francini 1990). MIMICRY: this species was included in the "orangish red mimicry complex" of Francini (1989) and "*alalia* mimicry complex" of Brown and Francini (1990).

Actinote quadra Schaus
(Fig. 4 p–s)

Acraea quadra Schaus 1902:392;
Actinote quadra Jordan 1913b:373; Jordan and Eltringham 1913:13; Jordan and Eltringham 1916:18; Lewis 1975:227; Smart 1976:265; D'Abrera 1987:445; Brown 1987:41; Brown 1988:36; Francini 1989:41 and several other pages; Francini 1992:25 Fig. 6–14 [QUA].
Acraea (Actinote) quadra Pierre 1987:22.

Diagnosis. Hindwing under surface whitish yellow, pale and homogeneous, lacking dark brown marginal shading; dark-colored scales restricted to wing veins. Forewing elongated at the tip, with a line of dark scales parallel to its whole basal area, resembling a wing vein. *Male genitalia* (Fig. 4 p–r): with extremely bowed valvae, unique among southeastern Brazil *Actinote* species. *Female genitalia* (Fig. 4 s).

Biology. HOSTPLANTS: unknown. IMMATURES: unknown. TOXICITY: unknown. MIMICRY: although preserved specimens of *A. quadra* suggest that this species is a member of the orangish red mimicry complex, when observed in flight (R.B.F. pers.obs.) it appears that this species belongs to a distinct mimicry complex that is the subject of a future study.

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OCCURRENCE OF TWO PALAEARCTIC SPECIES OF *CLEPSIS* GUENÉE, *C. SPECTRANA* TREITSCHKE AND *C. CONSIMILANA* (HÜBNER) (TORTRICIDAE), IN BRITISH COLUMBIA, CANADA

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ABSTRACT. The occurrence in North America of two species of *Clepsis* Guenée native to Europe and part of Asia, *C. spectrana* Treitschke and *C. consimilana* (Hübner), is reported. Diagnoses, descriptions of adults, and illustrations of wing patterns and male and female genitalia are provided for identification of these two species in North America.

Additional key words: distributional records, host range, genitalic illustrations.

Clepsis spectrana Treitschke is of Palaearctic origin, widely distributed from England through most of Europe and extending east as far as Turkey, trans-Caucasus, and Kazakhstan. Recently, a number of specimens of this species were collected in British Columbia, Canada, on cultivated raspberry, currant, white spruce, and white cedar, prompting this report. A single specimen of this species in the Canadian National Collection of Insects and Arachnids (CNC) was collected in 1950 from Abbotsford, British Columbia. Although *C. spectrana* evidently has existed in the Vancouver area for more than 45 years, it has remained unrecognized until today. This species is a prime candidate to become a serious pest in North America because its larvae are highly polyphagous. Various agriculture crops, such as blueberry, raspberry, currant, or even forest trees, such as species of spruce and cedar, could be seriously affected if an outbreak of this pest should occur. It is already an economically important pest of currants in Delta, British Columbia.

A second Palaearctic species, *C. consimilana* (Hübner), was recently discovered in British Columbia. The larvae were collected on *Taxus baccata* L. (Taxaceae) and reared through to adults. Although *C. consimilana* was reported in North America (eastern United States) many years

ago (Klots 1941), and fairly recently in Oregon (Powell 1986), its discovery in British Columbia is the first distributional record in Canada, and could well represent a recent introduction. This species was known by Klots (1941) as *Tortrix unifasciana* Duponchel and by Powell (1983) as *Clepsis unifasciana* (Duponchel). In Eurasia, *C. consimilana* has a distribution similar to that of *C. spectrana*; however, it has also been recorded from eastern Siberia and Madagascar (Bradley et al. 1973, Kuznetsov 1978).

MATERIALS AND METHODS

The present study is based on specimens from British Columbia, collected and reared by personnel of the Pacific Agriculture Research Centre, Vancouver, and the Pacific Region Canadian Forest Service. Four male specimens from the British Isles and two specimens (1♂, 1♀) of *C. spectrana* from Germany, and nine specimens (7♂, 2♀) of *C. consimilana* from England were also examined and compared to help confirm the identity of these specimens. All specimens examined are deposited in the CNC.

Selected adults were photographed to illustrate wing shape and patterns. Genitalia were dissected (Dang 1993), studied, and drawn while submerged in glycerin. They were then mounted on microscope slides in Canada balsam for preservation and storage. In the "Material Studied" sections below, the number in parentheses after the number of males or females indicates the number of genitalia dissected and examined.

The following descriptions are designed to assist forest and agriculture workers in North America identify these two non-native species of *Clepsis* so that dispersal, populations, and new host ranges can be monitored and, if required, necessary control measures can be effectively implemented.

Clepsis spectrana (Treitschke)

Tortrix spectrana Treitschke 1830. Schmett. Eur. 8:77.
Clepsis spectrana, Bradley, et al. 1973:122; Kuznetsov 1978:360; Razowski 1979:147.

Diagnosis. This species is superficially similar to the North American *C. fucana* (Walsingham), especially in the forewing color and markings. However, the forewing markings are more reddish brown; the medial fascia, in particular, is more uniformly colored in *C. fucana* as opposed to dark brown and darker and better defined anteriorly in *C. spectrana*; in addition to differences in markings, the costal fold is present in the male of *C. spectrana*, absent in *C. fucana*. Furthermore, these two species are easily distinguished from one another on the basis of the following genital differences: valva distinctly longer than wide, at least 1.5 times largest width, aedeagus entirely smooth, and corpus bursae with well-developed, clawlike signum in *C. spectrana*, as apposed to valva as long as wide, aedeagus with sharp teeth at subapical area, and corpus bursae without signum in *C. fucana*.

Description. Generally a light orange-yellow to light yellowish brown species with distinct dark brown, oblique medial fascia and costal spots. *Male*: length of forewing 8.0–10.5

mm. Head: Scales on vertex semierect, concolorous with ground color of forewing; antennal flagellum mostly pale, concolorous with vertex, dotted with scattered dark brown scales; labial palpus brown laterally and pale yellow mesally. Medial and laterodorsal areas of notum concolorous with ground color and marking color of forewing respectively. Forewing (Fig. 4A) fairly truncate apically with well-developed costal fold; ground color light orange-yellow to light yellowish brown; markings distinct, dark brown: medial fascia obliquely extended from one-third from base of costa to one-third from tornal angle of posterior margin, portion from costa to outer margin of discal cell well defined, dark brown, remaining portion fairly diffuse, lighter brown; basal margin of fascia somewhat jagged; subterminal fascia reduced to well-defined, large, subterminal, nearly semicircular, dark brown spot at costa; basal and subbasal areas nearly concolorous with ground color, occasionally slightly darker, brownish orange-yellow, except for mostly dark brown costal area along costal fold. In pale specimens, posterior portion of medial fascia, and laterodorsal area of notum nearly concolorous with ground color of forewing or medial region of notum resulting in forewing with overall pale orange-yellow ground color and two prominent dark brown costal spots. Hindwing fairly uniformly colored, pale yellow to light grayish yellowish brown. *Female:* without costal fold, otherwise mostly similar to male.

Male genitalia (Figs. 1A–D): uncus well developed and sclerotized, depressed, abruptly bent at base, L-shaped in lateral view, nearly parallel sided except for slight constriction near base, 4 times as long as greatest width, with numerous fine setae on dorsal and ventral sides; apex round. Socius moderately developed, with rectangular, well-sclerotized basal portion and small, short, fleshy, thumb-shaped, mesally directed, finely setose distal portion. Gnathos well developed and sclerotized, joined distomedially forming wishbone-shaped structure. Valva parabolic in outline, distinctly longer than wide; basal process well developed, moderately sclerotized, spherical, bearing numerous spines dorsally; sacculus well sclerotized, narrowed distally into sharp point. Aedeagus, well sclerotized, fairly straight, somewhat conical, widest anteriorly; posterior half obliquely tapered into sharp point apicoventrally. Vesica as long as aedeagus, cylindrical, with small, fleshy, finger-shaped distoventral, ventrally-directed diverticulum and with cluster of 5 large, slender, attenuate spindle-shaped, and 3–4 thinner, seta-shaped cornuti loosely clustered at around right laterodistal and distal areas just dorsad of diverticulum; gonopore located distodorsally.

Female genitalia (Figs. 3A–Aa): Anal papillae elongate, foot-shaped, somewhat tuberculous, with fine setae. Sterigma weakly sclerotized, trapezoidal, much wider posteriorly. Ostium bursae round. Antrum narrow anteriorly, mostly membranous except lateral sides of anterior half thickly sclerotized with microscopic transverse ridges; inner surface of dorsal side of posterior half with posteriorly directed spicules. Ductus bursae anterad of antrum narrow, cylindrical, membranous, 4 times as long as anal papillae. Corpus bursae small, irregular potato-shaped, membranous. Signum large, well sclerotized, compressed, claw-like with finely serrate inner edge.

Material Studied. CANADA: BRITISH COLUMBIA: Pitt Meadows, 31.V.1950, (blueberry), 1♀ (1), D. Gillespies; Abbotsford, 22.IV.1991, (reared from *Picea glauca*), 1♂ (1), 1♀ (1), R. Duncan; Maple Ridge, IV.1994, (reared from *Thuja occidentalis*), 1♂, R. Duncan; Abbotsford, 5–10.III.1992, (reared from currant), 3♂; 11.V.1993, (reared from raspberry), 1♂, J. Troubridge; Lower Fraser Valley, IV.1993, (reared from currant), 2♀, 5♂, S. Fitzpatrick. ENGLAND: Oxford, 1890, 3♂; 1900, 1♂. GERMANY: Lichterfelde, Mark Brendenburg, 25.VI.1929, 1♂ (1), 1♀ (1), (on *Epilobium hirsutum* L.), H. G. Amsel.

Biology. In Europe and western Asia, this species has been reported to feed on grape, *Spiraea, Potentilla, Aster, Urtica, Euphorbia, Cicuta, Epilobium, Comarum,* comfrey, sorel, iris, cypress, field cress, and most herbaceous plants in semi-aquatic habitats such as fens and marshes, and on cultivated plants, such as *Cyclamen,* strawberry, hops and *Pelargonium* (Bradley et al. 1973, Kuznetsov 1978, Razowski 1979). In British Columbia, the larvae have been reared on or collected from white spruce, white cedar, blueberry, raspberry, and currant. Adults are nocturnal and readily attracted to lights. In Europe, adults fly during May–July; in British Columbia, adults are found from late March until early August. Larvae found in March apparently belong to the fall generation of the previous year that overwintered; those found from May to August represent current year generations. There are 2–3 generations a year in British Columbia.

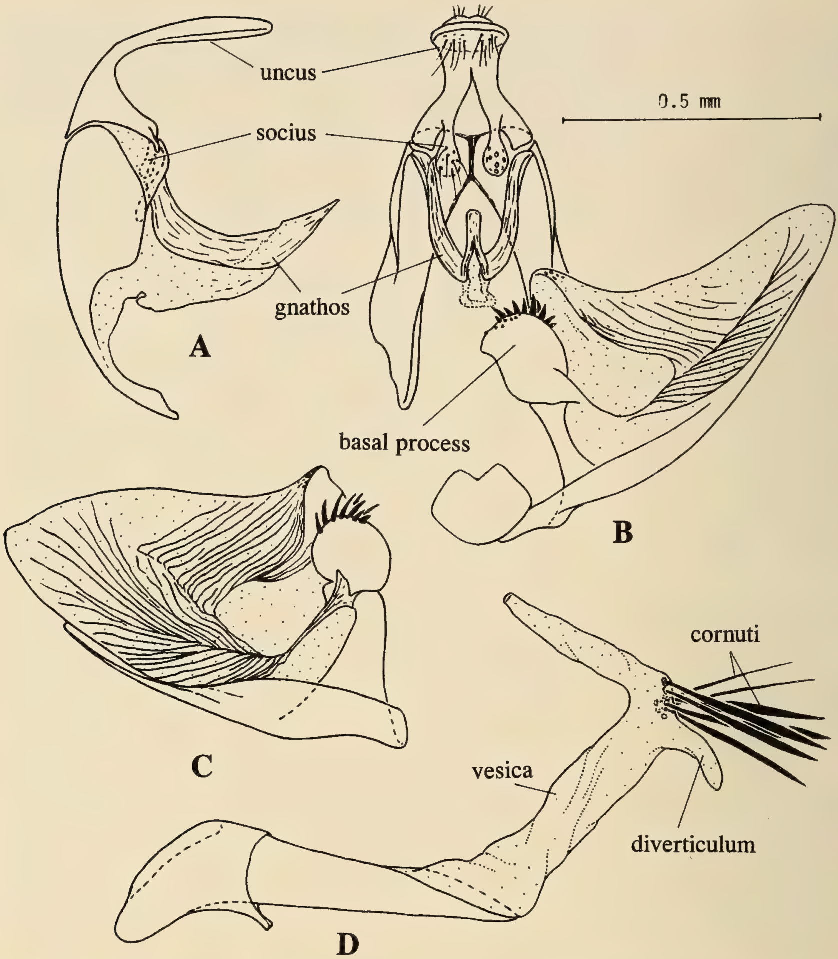

FIG. 1. Male genitalia of *Clepsis spectrana* (Treischke). A, lateral aspect of dorsal components of genitalia; B, posteroventral aspect of genitalia with left valva and aedeagus removed; C, mesal aspect of left valva; D, lateral aspect of aedeagus.

Clepsis consimilana (Hübner)

? *consimilana* Hübner (1814–1817). Samml. eur. Schmet., tab. 38, fig. 239.
Clepsis consimilana, Bradley et al. 1973:124; Kuznetsov 1978:363; Razowski 1979:162; Powell 1986:165.

Diagnosis. *Clepsis consimilana* is distinguished from its North American counterparts by the deep brown and immaculate, or nearly so, forewing, and by the structure of the genitalia.

Description. Generally a deep brown, immaculate, or faintly marked species. *Male*: length of forewing 7.5–9.0 mm. Body scales, including those on vertex, antennal scape and flagellum, labial palpus, notum, and forewing nearly uniformly deep brown. Forewing

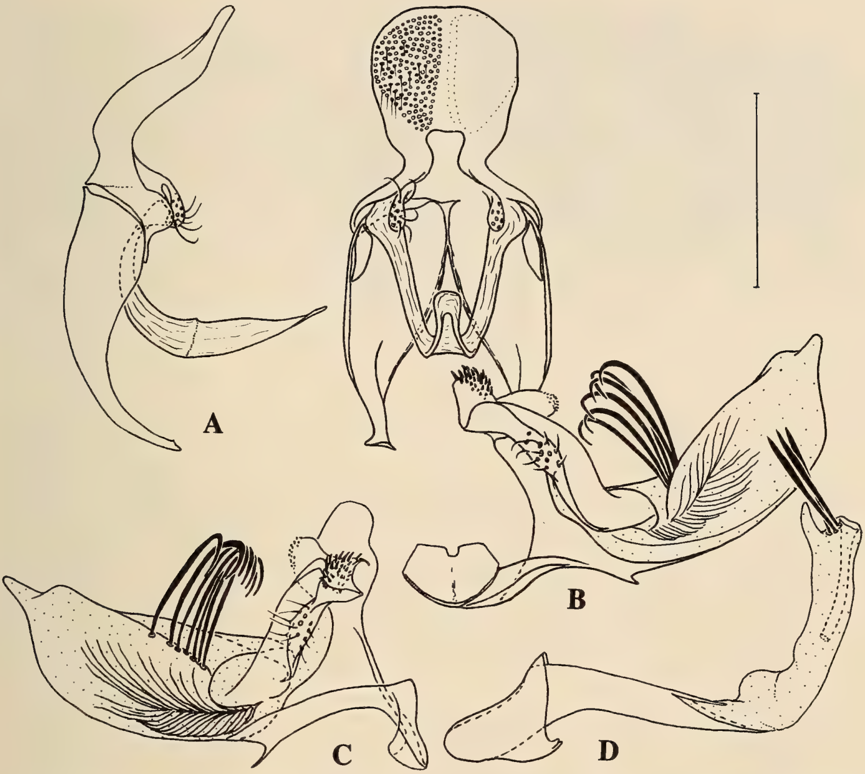

FIG. 2. Male genitalia of *Clepsis consimilana* (Hübner). A, lateral aspect of dorsal components of genitalia; B, posteroventral aspect of genitalia with left valva and aedeagus removed; C, mesal aspect of left valva; D, lateral aspect of aedeagus.

(Fig. 4B) slightly oblique terminally; costa straight with developed costal fold; immaculate, deep brown in most areas except for areas distad and posterad of anterior margin of discal cell with dominant dark grayish brown scales. Hindwing fairly uniformly dark grayish brown. *Female*: without costal fold, otherwise mostly similar to male.

Male genitalia (Figs. 2A–D): uncus well developed and sclerotized, depressed, distinctly bent at base, short and wide, gradually but distinctly broadened apically, 1.5 times, or less, as long as greatest width, with numerous fine setae on both ventral and dorsal surfaces except along medial areas; apex round. Socius small, mesally directed, with fusiform, well-sclerotized basal portion, and fleshy, short, thumb-shaped distal portion, as long as basal portion, with fine setae. Gnathos well developed and sclerotized, joined distomedially, forming wishbone-shaped structure with duck bill-shaped common medial process in posterodorsal view. Valva narrow, subrectangular, 2.5 times as long as width, with following diagnostic features: (a) small, fleshy, conical process at distal end; (b) row of conspicuously large, compressed, strongly curved, heavily sclerotized, mesally directed setae extending medially from base to about midlength of valva; and (c) basal process large, well developed and sclerotized, armlike, directed anteromesally, and reaching opposite counterpart medially; distal end of process hemispherical, with coarse, barblike spines dorsally; sacculus small, well sclerotized with small spinelike process ventrally. Aedeagus well scle-

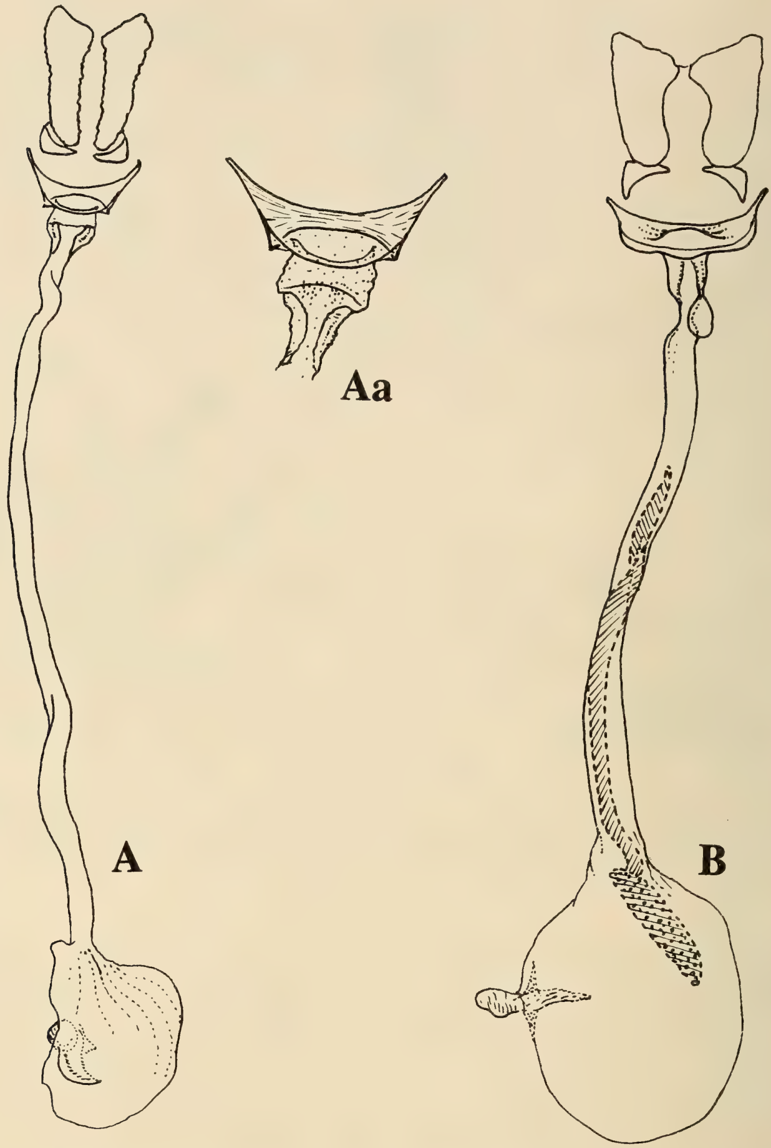

FIG. 3. Female genitalia. A, ventral aspect of genitalia of *C. spectrana*; Aa, sterigma region of *C. spectrana;* B, ventral aspect of genitalia of *C. consimilana*.

rotized, slender, fairly straight, wider anteriorly; dorsal one-third of aedeagus from apex produced apically into slender, spine-shaped, appressed process, nearly reaching apex; distal third obliquely tapered into sharp point apicoventrally. Vesica as long as aedeagus, fairly simple, cylindrical, with small finger-shaped, distodorsal diverticulum, and cluster of 3

FIG. 4. Adults: A, *C. spectrana*; B, *C. consimilana.*

slender, large, seta-shaped, distally located cornuti; gonopore located just ventrad of cornutus cluster.

Female genitalia (Fig. 3B): Anal papillae short foot-shaped, with fine setae. Sterigma weakly sclerotized, trapezoidal, much wider posteriorly. Ostium bursae round. Antrum narrow anteriorly, mostly membranous, smooth. Ductus bursae anterad of antrum narrow, cylindrical, 4 times as long as anal papillae, membranous, with sclerotized ribbonlike plate, extending from posterior one-third from antrum to posterior portion of corpus bursae, ending in elongate oval plate with numerous round bumps covering inner surface. Corpus bursae small, spherical, membranous. Signum large, well sclerotized, compressed, claw-like with serrate inner edge, and with prominently protruded proximal end.

Remarks. There are two color forms, one with immaculate forewing and the other with faintly visible medial fascia.

Material Studied. CANADA: BRITISH COLUMBIA: Saanichton, 3.VI.1993, (reared from *Taxus baccata* L.), 4♀, 1♂ (1), R. Duncan; 24.VI.1994, (reared from *Taxus baccata* L.) 2♂ (1), 1♀ (1), R. Duncan. ENGLAND: Sydenham, VII.1892, 7♂ (2); Purback, 2.VII.1899, 2♀ (1).

Biology. Larvae feed on privet and lilac (Europe and eastern United States). In British Columbia, the larvae were collected and reared from *Taxus baccata* L. (an unusual host) where they were found associated with *Argyrotaenia citrana* (Fernald) in large accumulations of webbing and chewed needle fragments; the flight period of the adults has not been fully recorded, but at least is known to occur throughout June.

ACKNOWLEDGMENTS

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DESCRIPTIONS OF THE IMMATURE STAGES OF *ADELPHA ALALA* (NYMPHALIDAE)

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Abstract. Descriptions of the morphology and behavior of the immature stages of *Adelpha alala* are given. *Adelpha alala* does not fit into any of the species groups of *Adelpha* yet recognized. *Viburnum tinoides* var. *venezuelense* (Caprifoliaceae) is its larval host plant, documenting a new host plant family for the genus *Adelpha*.

Additional key words: Venezuela, pupa, *Viburnum tinoides*, Caprifoliaceae.

Relationships among the 100 or so species of butterflies included in the genus *Adelpha* Hübner (Nymphalidae) long remained a puzzle for butterfly taxonomists. The traditional approach to butterfly classification, using adult wing pattern characters proved useless in arriving at a satisfying arrangement (see references in Aiello 1984). Recent contributions (Aiello 1984, 1991) follow what seems an appropriate course toward the clarification of taxonomic relationships within the genus, building a consistent picture from characters of early stages and information on life histories. Aiello (1984) proposed that *Adelpha* butterflies can be assigned to at least seven groups based on pupal and larval morphology. Interestingly, while groups I, II and III are rather unorthodox in their larval host plant relationships, using plants from a number of different families, *Adelpha* species in the remaining groups, IV–VII, are reported to use plants of the family Rubiaceae, except for one or two doubtful records, a host-use pattern that in itself is suggestive of a natural grouping; or it may be sympleisiomorphic.

In the following account we describe the early stages of a Venezuelan species, *Adelpha alala* Hewitson, report observations on its behavior, review the phylogenetic position of the species within the genus, and report *Viburnum tinoides* var. *venezuelense* (Killip & Smith) Steyermark (Caprifoliaceae) as the larval host plant, adding a new larval host plant family to those previously recorded for *Adelpha*.

MATERIALS AND METHODS

On 10 May 1992, a female *Adelpha alala* was seen flying insistently around a small *Viburnum tinoides* tree in Monterrey, El Valle, near the city of Mérida, Venezuela, at an elevation of about 2350 m. A search

among the foliage produced one egg, recently laid on the under side of a leaf, and three early instars. All were reared to adults (Fig. 1), except a first instar, which died shortly after emerging from the egg. Since then, early stages of the species have been collected and reared on several occasions, allowing the preservation of immatures and adult vouchers.

Larvae and eggs collected in the field were taken to the lab with the leaf and a part of the branch on which they were found. Once in the lab, the branch was anchored in a small glass flask filled with water and placed on a plastic dish covered with an inverted one-liter plastic container. Fresh foliage was provided when necessary, and accumulations of frass and fecula were discarded regularly. Larval and pupal exuviae were saved and pinned with the specimens. Vouchers of the butterfly were deposited in the Museo del Instituto de Zoología Agrícola (MIZA) and vouchers of the plant (*L. D. Otero 66* and *L. D. Otero 203*) in the Herbario de La Facultad de Agronomía (MY) of the Universidad Central de Venezuela, both in Maracay, Edo. Aragua, Venezuela.

RESULTS

Viburnum tinoides is the larval host plant of *Adelpha alala* in Venezuela. The plant, a shrub or small tree commonly known in Venezuela by the name of "Cabo de Hacha," is usually distributed at elevations of 1000 to 3000 m and is a rather common species in forest margins and secondary vegetation in the Mérida area. According to Steyermark (1953), four varieties of *V. tinoides* are the only *Viburnum* occurring in Venezuela; *V. tinoides* var. *venezuelense* (Killip & Smith) Steyermark is the variety commonly encountered in the Mérida area.

Early Stages

Egg. The eggs of *A. alala* are typical of the tribe Limenitidini and closely resemble the egg illustrated in Aiello (1984). They are approximately hemispherical, and are yellowish white in color, but the most characteristic feature is their sculpturing, which consists of concave hexagonal facets joined by their sides and vertices. A sharp pointed structure projects from each vertex. The eggs are laid singly on the under surface of the leaf. The first instar eats an escape hole in the egg, but does not consume the entire shell.

Larva. The first instar is dull green and grows to about 5 mm in length. The head capsule is rugose and paler than in later stadia. The second instar shows two colors: a wide, dorsal, greenish yellow stripe divided longitudinally by a thin median line, and a lateral maroon stripe bordered below by a white subspiracular line. The general pattern, with perhaps slight changes in hues, is maintained through the fourth instar and is present still in the recently molted fifth instar. As the fifth instar (Figs. 2, 4) matures, it becomes a rather uniform green, except for the white subspiracular line and a paler green below it. The body is clothed in greenish chalazae.

Compared with the larvae of other *Adelpha* species, *A. alala* displays a rather simple ornamentation. Most body segments are free of scoli or, at most, have clusters of minute spines in place of subdorsal scoli. Segments T2, T3, and A8 bear true scoli, all round in cross section and subdorsal in position. Those of T2 are the largest, and are orange with

FIGS. 1–3. *Adelpha alala*. **1,** Adult, dorsal (above) and ventral (below) (wingspan 48 mm). **2,** Mature larva (30 mm long). **3,** Leaf shelter (leafy portion 8 mm long) constructed by larva on *Viburnum tinoides*.

one black spine at the middle and five radiating black spines at the apex. The scoli of segments T3 and A8 are very small.

Pupa. The pupa (Fig. 5) is bone white to straw colored. The dorsal, thoracic (T2) and abdominal (A2) projections are small, with that of A2 slightly larger than that of T2 and ending in a short point directed anteriorad. The small, triangular head horns are directed to the sides. In general form, it is similar to the pupae of *Adelpha justina* (C. & R. Felder) and *A. jordani* Fruhstorfer, although it displays neither the silver markings of the former nor the black markings of the latter. Also unlike the pupa of *A. justina*, which is oriented horizontally (dorsal side down), the pupa of *A. alala* hangs head down as do other *Adelpha* species and most other Nymphalidae. Pupal orientation for *A. jordani* is not known.

Behavioral Notes. Characteristic of many nymphalids, *Adelpha* larvae utilize leaf veins to construct resting perches (Moss 1933, Aiello 1984). First instars strip a leaf vein, the midrib in the case of *A. alala*, by eating the surrounding tissue. They then extend the newly exposed perch by adding fecal pellets held in place by silk (see description in Aiello 1984; see Muyshondt and Muyshondt 1979, for perch construction by other nymphalids).

Late first instar and second instar *A. alala* go on to construct elaborate shelters, a behavior not reported previously for any other *Adelpha*. Shelter construction by *A. alala* begins with two opposing cuts, each at, and perpendicular to, the leaf margin, and ending at the midrib. The larva pulls the resulting symmetrical flaps of leaf downward, curving them beneath the leaf, and fastens their proximal edges together with silk to form a tepee-like shelter which opens towards the apex of the leaf (Fig. 3). The larva resides inside the shelter when not feeding, until well into the fourth stadium. Usually, the shelter entrance has a curtain of small pieces of leaf tissue left dangling by the first instar as it fed from the distal end of the leaf.

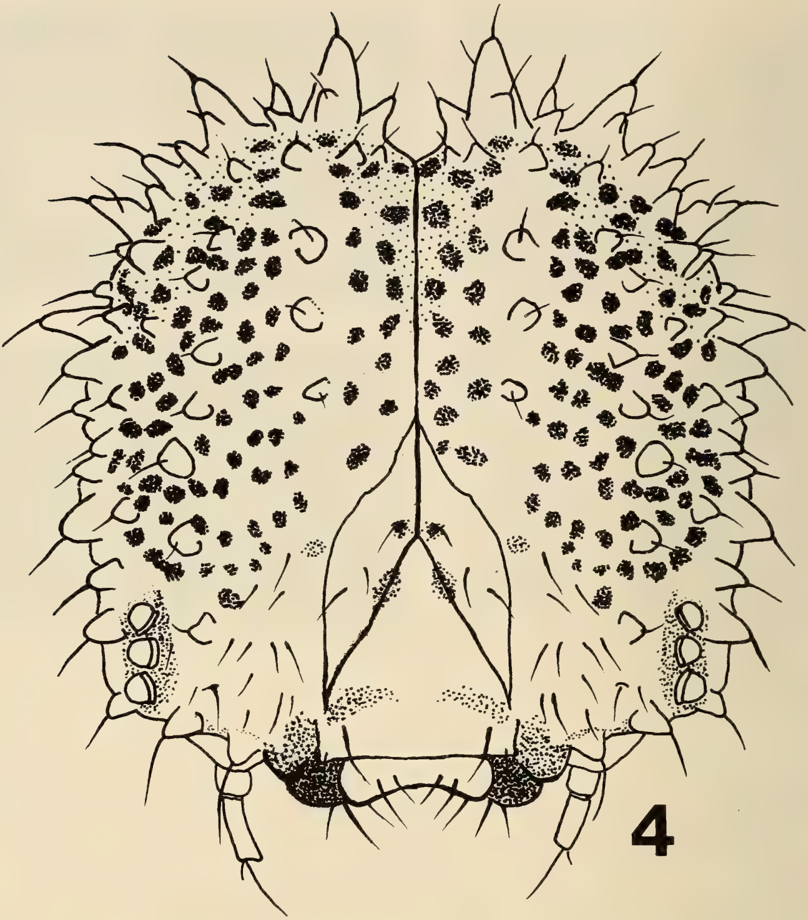

FIG. 4. *Adelpha alala*. Head capsule (3 mm wide) of mature larva.

If the shelter is assumed to play a defensive role, it might be supposed that the earlier the shelter is constructed, the more important its function as a protective structure. In the lab, we have recorded cases in which shelter construction was completed by the second instar, which is most likely what occurs in the field on leaves that have not been perturbed by removal from the plant. In other cases we observed larvae begin shelter construction more than once because their original leaf had decayed. In some cases construction was completed by the third instar. Once finished, the larva crawls into the shelter during periods of inactivity and curls up against the inner walls, a habit that continues into the advanced fourth or early fifth stadium, by which time the head capsule and posterior end of the curled larva begin to protrude from the opening. The shelter is abandoned by the larva either just before molting to the fifth stadium or shortly afterwards, and from then on it lives exposed on leaves. Interestingly, during the final stadium, the larva turns green.

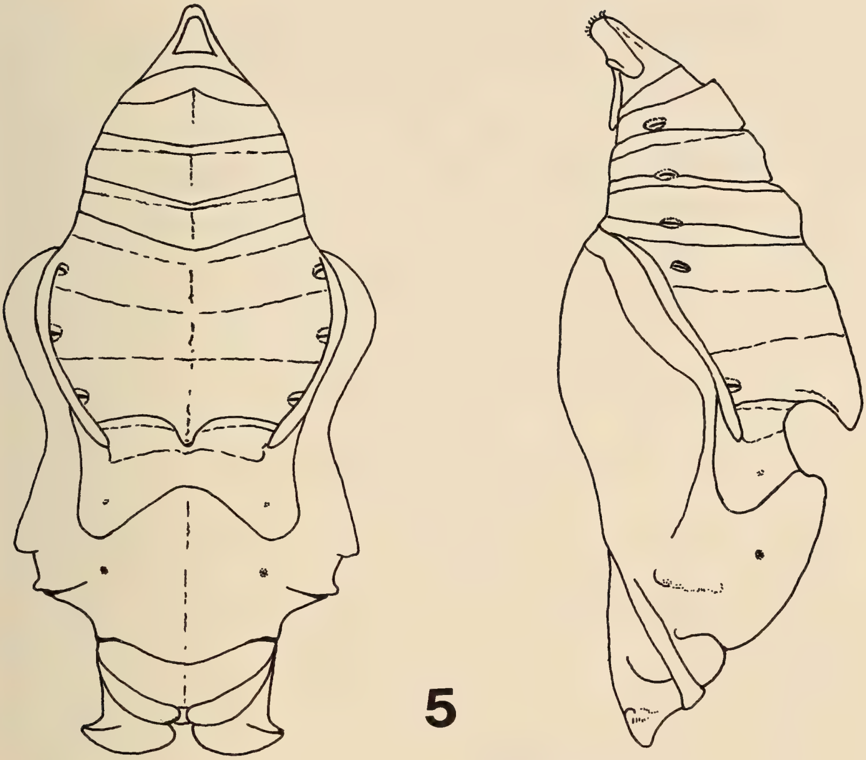

FIG. 5. *Adelpha alala*. **5,** Pupa (2 cm long), dorsal (left) and right side (right).

DISCUSSION

The larva of *A. alala* differs from larvae of other *Adelpha* species in having greatly reduced body scoli. Larvae of *A. justina* and *A. jordani* have somewhat reduced scoli, but nevertheless do retain those structures on most abdominal segments. In contrast, the larva of *A. alala* lacks scoli on most abdominal segments, and the few scoli that are present (on segments T2, T3, A8) are quite reduced, giving the larva a nearly bare appearance. In general aspect, it does not resemble closely any other *Adelpha* species for which the larva is known.

In addition, the habit of constructing a larval shelter has not been reported for any other *Adelpha* species. In the Old World, however, *Ladoga (Limenitis) camilla* L. (Nymphalidae), and *Ladoga (Limenitis) reducta* Staudinger overwinter within shelters constructed by joining the edges of a leaf together with silk (Carter 1982). Interestingly, the larval host plant of both those species is *Lonicera*, also of the Caprifoliaceae.

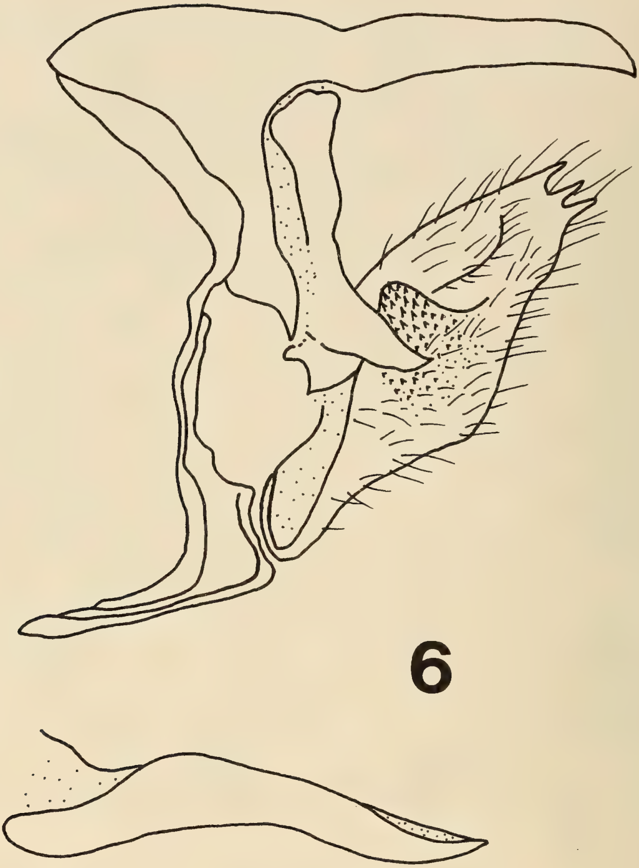

FIG. 6. *Adelpha alala*. Male genitalia.

It is doubtful that *A. alala* belongs to any of the seven *Adelpha* species groups outlined by Aiello (1984). Possibly, it represents an eighth group. As the immatures and larval host plants of more species are discovered, perhaps other *Adelpha* species with larvae similar in form and behavior to that of *A. alala* will reveal themselves. Judging from the genitalia (Fig. 6), other species that potentially belong to the same group as that of *A. alala* may include *A. aricia* Hewitson, *A. corcyra* Hewitson, *A. donysa* Hewitson, *A. pithys* Bates, and *A. tracta* Butler, with which *A. alala* shares: the clunicula broad and not reaching the costal margin; the valve lacking a costal bulge; and the valve apex armed with 1 to 3 large distinct spines. Unfortunately, none of these species has been reared. Genitalic drawings, by Howarth, for more than 70 species of *Adelpha* are included

in an uncompleted manuscript by Forbes (archives of the Museum of Comparative Zoology, Harvard University). Forbes concluded that genitalia were not helpful in classifying *Adelpha* species because they did not agree with the wing patterns.

At present, *Viburnum* is generally considered to belong to the family Caprifoliaceae, order Dipsacales, subclass Asteridae (Takhtajan 1980, Cronquist 1981), although recently the affinities of the genus have been called into question by Donoghue et al. (1992), who, based on chloroplast nucleotide sequences, concluded that the Caprifoliaceae do not form a monophyletic group and that *Viburnum* does not fit with Caprifoliaceae *sensu strictu*. *Viburnum tinoides* var. *venezuelense* represents an addition of both a larval host plant species and a family to the plant associations recorded for *Adelpha* (Aiello 1984, Ackery 1988).

While obvious progress has been made in our understanding of systematic relationships within the genus *Adelpha*, life history information, much of it incomplete, has been reported for only a portion of the approximately 100 species. We urge others to seek the immature stages of additional species and to publish illustrated accounts of their findings. As well, we have only a vague understanding of the relationships between New and Old World members of the tribe Limenitidini. It is possible, for example, that *Adelpha* actually represents several genera, and that some of those genera may be more closely related to Old World genera than to each other. Whether molecular studies will clarify the complex relationships within the Limenitidini remains to be seen, but certainly that approach should be taken by anyone who has access to the appropriate facilities and to fresh subject material.

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THE IMMATURE STAGES OF *PHARMACOPHAGUS ANTENOR* (DRURY) (PAPILIONIDAE: TROIDINI) FROM MADAGASCAR

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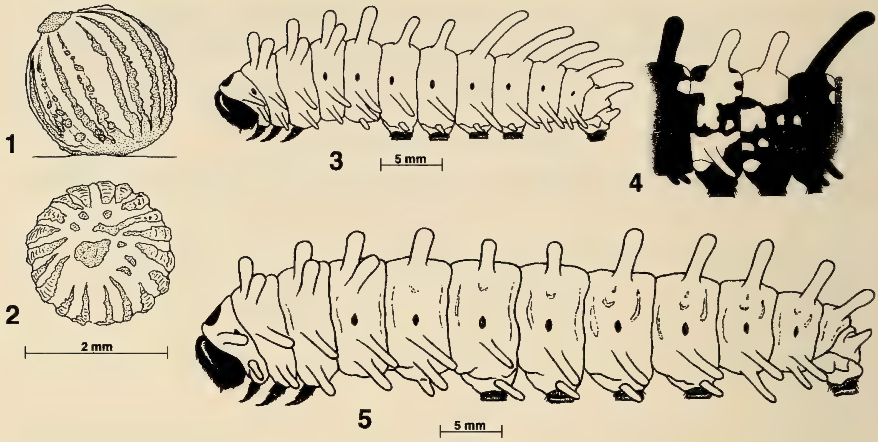
ABSTRACT. The early stages of *Pharmacophagus antenor* from Madagascar are described and illustrated in detail for the first time. They confirm that *Pharmacophagus* differs from Indo–Australian Region *Atrophaneura*, and suggest that the morphological relationships of the genus lie elsewhere within the tribe Troidini.

Additional key words: afrotropical, *Atrophaneura*, larva, ovum, pupa, swallowtail.

Pharmacophagus Haase, 1891, contains the single species *antenor* (Drury 1773). This monotypic Madagascan genus is biogeographically important, as *P. antenor* is the only representative of the swallowtail butterfly tribe Troidini in the entire Afrotropical Region. Taxonomically and systematically, the status of *Pharmacophagus* remains open to speculation. The taxon has been considered to be of generic rank by some authors, but authors such as Hancock (1988) and Miller (1987) have regarded it as warranting only subgeneric rank under *Atrophaneura* Reakirt. Based on the morphological characters of its immature stages, I consider *Pharmacophagus* represents a distinct genus and, using these data, have treated its taxonomic and phyletic status in greater detail elsewhere (Parsons 1996). Like almost all of its troidine relatives in eight other predominantly pantropical genera, *P. antenor* is restricted to larval foodplants of the family Aristolochiaceae. These plants, also mostly pantropical, number about 500 species, the majority of which are large vines or lianas of the genus *Aristolochia* (e.g., Hou 1984).

Preston-Mafham (1991) provided a good color photographic plate of a *P. antenor* adult male and female in copula. He noted that the species is common and widespread over much of Madagascar (e.g., Ampijeroa Forest Reserve), often flying strongly at quite a height. On one occasion, the author "mistook one for a bird as the insect powered strongly along the beach on the hot dry coast at Morondava" (the locality approximately centrally situated on the Madagascan west coast, almost opposite the east coast capital of Antananarivo). Preston-Mafham suggested that "with its widespread distribution and lack of fussiness over habitat, this magnificent butterfly is not under imminent threat from environmental changes by humans."

The immature stages of *P. antenor* were briefly described by Denso (1943), and Igarashi (1984) provided a basic sketch of the pupa. Since Denso's paper, apparently no other accounts of the early stages of *P. an-*



FIGS. 1–5. Early stages of *P. antenor* (line drawings) **1.** Ovum: lateral. **2.** Ovum: dorsal. **3.** Fourth instar larva: lateral. **4.** Fourth instar larva detail of saddle markings: lateral. **5.** Fifth instar larva: lateral.

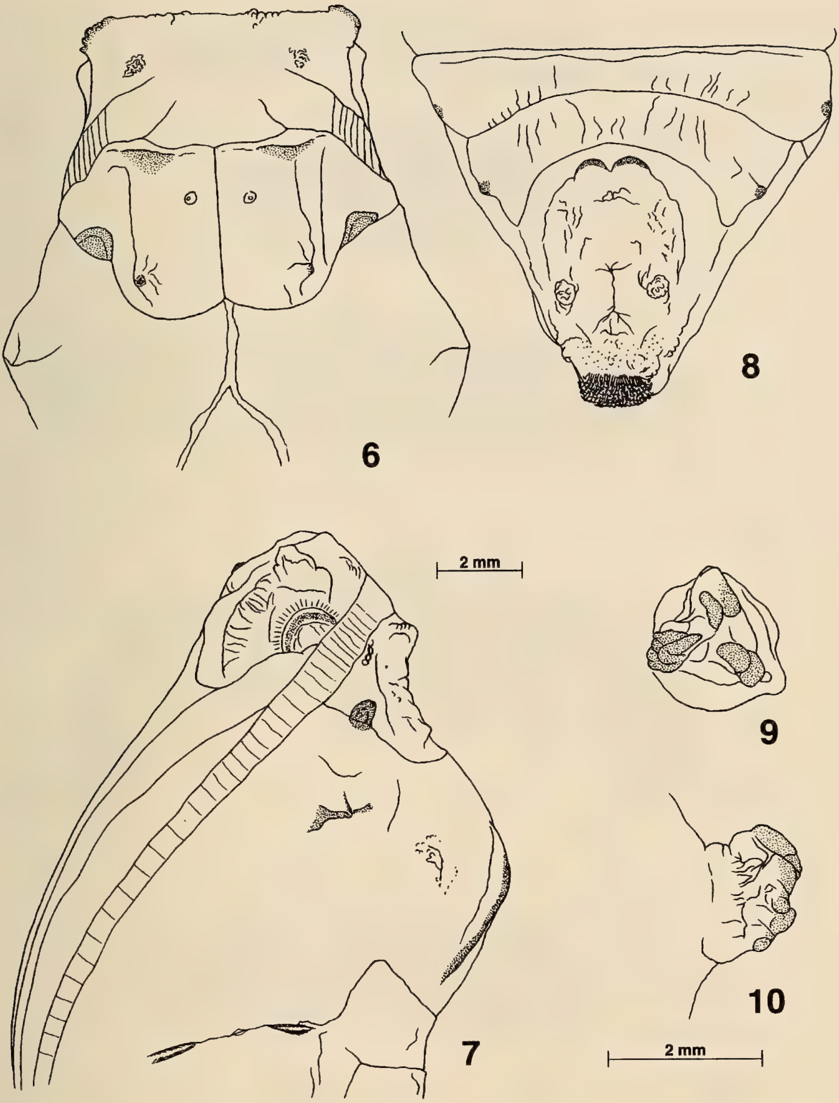
tenor have been published, hence the account and illustrations provided below. The material from which the descriptions are made was kindly provided to me by A. Peyrieras who, in 1979 while at the Department Recherché Scientifique et Technical in Antananarivo, Madagascar, sent me alcohol-preserved *P. antenor* immature stages. This included both wild-collected and captively-reared specimens, all material having been taken in the immediate area of Antananarivo.

IMMATURE STAGES

Egg. (Figs. 1 and 2). Circa 2.0 mm in diameter, spherical, but slightly basally flattened, chorion white, covered with thin layer of pinkish, wax-like glue which affixes ovum to substrate, glue forming ca. 19 thick granulose ribs, and a thick apical "cap." Based on the specimens on preserved leaves received, eggs are laid on the underside of a leaf of the foodplant, as is typical of many troidines.

Larva. The "saddle mark" typical of Troidini is present on abdominal segments (AS) 3 and 4, and is uniquely macular in *P. antenor* (Fig. 4). Although somewhat variable, it is similar through instars 2–4, comprising wholly white subdorsal tubercles on AS 3 and 4, their bases broadly white and middorsally just touching, or nearly so, white lateral tubercles on AS 3, white blotches of various sizes laterally on AS 3 and 4. Other smaller, more rounded white spots are usually present elsewhere on the body, notably forming rows of 4 across the back of the larva, these most prominent in the fourth instar on the posterior margins of the mesothoracic segment and AS 2 and 5 (Fig. 13). Otherwise the larva is as follows:

First instar: unavailable. *Second instar* (Fig. 11): ca. 13 mm long, saddle markings as above, typically troidine in shape and configuration of fleshy tubercles (8 rows on thoracic segments and AS 1–2; 6 rows on AS 3–10), subdorsal tubercles longest, body dark pinkish-brown, slightly paler on anal segments, prothoracic plate glossy black; head glossy black, sparsely hirsute. *Third instar* (Figs. 12, 16, 17): ca. 25 mm long, similar to second instar,



FIGS. 6–10. Pupa of *P. antenor* (line drawings). **6.** Detail of prothorax and head: dorsal. **7.** Detail of thorax and head: lateral. **8.** Detail of anal segments and cremaster of male: ventral. (In the female, abdominal segment 9 is ventromedially divided by a vertical line). **9.** Detail of dorsolateral abdominal tubercle (segment 5): dorsal. **10.** Ditto: lateral.

but ground color darker, more purple, and subdorsal tubercles on saddle segments AS 3 and 4 distinctly shorter than the rest. *Fourth instar* (Figs. 3, 4, 13): ca. 40 mm long, similar to third instar, but ground color dark brown, almost black, subdorsal tubercles on AS 5–9 somewhat longer and apically slimmer than rest, but decreasing in length posteriorly.

Fifth instar (Figs. 5, 14, 15): ca. 58 mm long, similar to fourth instar, but apparently uniform dark brown (based on the single alcohol-preserved specimen of this instar), all subdorsal tubercles distinctly apically rounded and mildly club-like.

The distinctly shorter subdorsal abdominal tubercles on segments 3+4, and club-like subdorsal tubercles in the final instar larva of *Pharmacophagus*, are specializations (or autapomorphies) among the tribe Troidini. Although Cuban *Battus devilliers* (Godart 1823) also possesses club-like subdorsal tubercles (color plate 31a in Tyler et al. 1994), this is a specialization at the species (rather than genus) level, as all other known *Battus* larvae possess tubercles with the plesiomorphic tapered condition.

Pupa. (Figs. 6–10, 18–20). Circa 43 mm long and 17 mm wide (male ca. 40 mm long, 16 mm wide), distinctly S-shaped in lateral profile, fairly stout and ovate in dorsal profile, wing cases large, very prominently and smoothly convex ventrally, frontal margin truncate, almost straight with only very small, truncate dorsolateral projections above eyes, prothorax concave in lateral profile, mesothorax with a pair of small lateral tubercles, abdomen with 3 pairs of bluntly truncate, irregularly deltoid and nodular dorsolateral tubercles on segments 4–6, decreasing markedly in size, 2 further low and rounded, vestigial pairs of dorsolateral tubercles on AS 7 and 8, AS 4 with a low, rounded lateral flange-like projection, ground color pale yellowish-brown, ventrally (wings, legs) with irregular blotches of dark brown melanin, metathorax and AS 1–4 dorsally with a "saddle-marking" of posteriorly diverging dark brown lines, between these a uniformly unmarked area of pale yellowish-brown, region outside lines and bounded by dorsal margin of wings with a fine tracery of irregular dark brown lines, continuing laterally and ventrally onto abdomen. A typical metathoracic girdle and thick mat of strong black silk supports the pupa. Duration 14 days (Denso 1943).

The form of the *P. antenor* pupa is unique for the tribe Troidini. In particular, the bluntly truncate, irregularly deltoid and nodular form of the dorsolateral abdominal tubercles (Figs. 9, 10) is unique to *antenor*. In all other Troidini (e.g., Figs. 21, 22) the tubercles are tapered, even when they are slightly truncate or spatulate.

FOODPLANT NOTES

Pharmacophagus antenor is monophagous on *Aristolochia acuminata* (Aristolochiaceae) (Denso 1943, A. Peyrieras pers. comm. 1979). Study of the literature, and herbarium material (e.g., pers. obs. at the Royal Botanic Gardens, Kew, Richmond, United Kingdom) suggests that this is the only *Aristolochia* species in Madagascar. The vine occurs in areas of marginal vegetation and has glabrous, heart-shaped leaves typical of its genus. Its flower is also typical, with a tubular, unilabiate perianth. On the moist west coast of Madagascar, *A. acuminata* does not lose its leaves and *P. antenor* flies there all year round (Denso 1943). However, in the seasonally dry south of the island, leaves of *A. acuminata* are shed between May and June with new leaf growth by the end of October; and Denso recorded that in the south, *P. antenor* undergoes an aestivative

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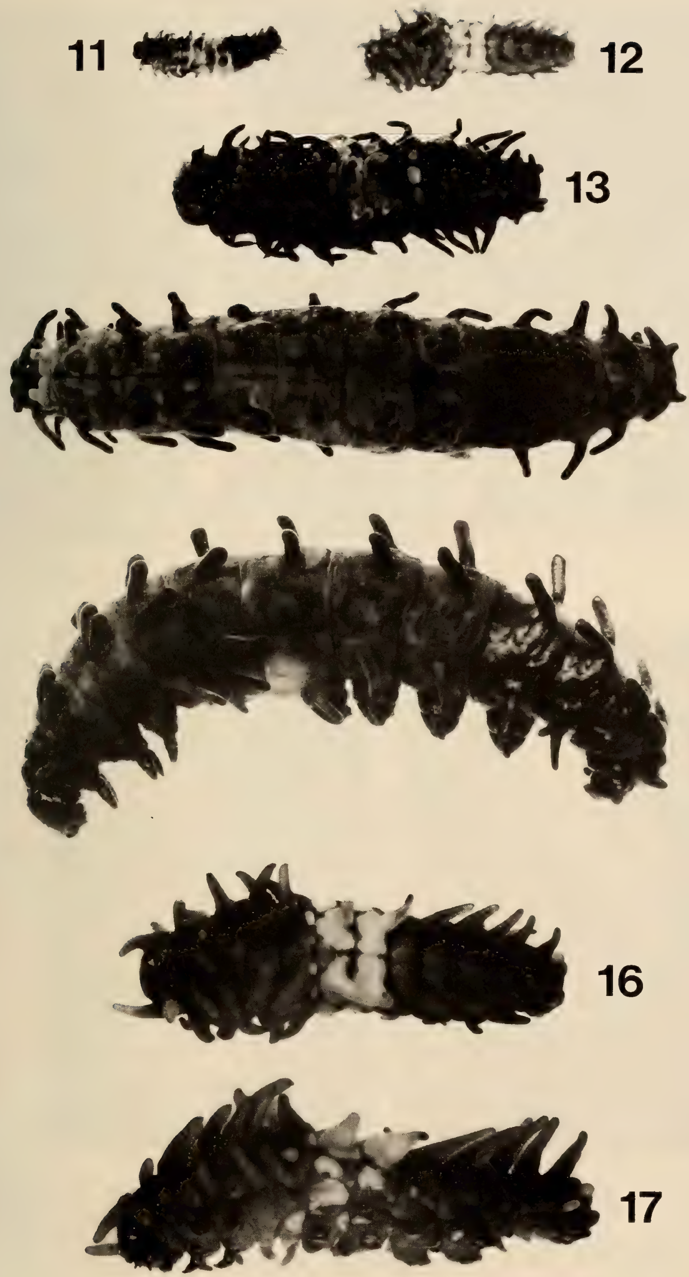
FIGS. 11–17. Larva of *P. antenor* (photographs 11–15 represented at same scale; 16 and 17 at different scale. Larval heads to left). **11.** Second instar: dorsal. **12.** Third instar: dorsal. **13.** Fourth instar: dorsal. **14.** Fifth instar: dorsal. **15.** Fifth instar: lateral. **16.** Third instar: dorsal (note saddle detail). **17.** Third instar: lateral (note saddle detail).

11  12

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FIGS. 19–22. Pupa of *P. antenor* compared to those of other Troidini (photographs). **18.** *P. antenor* (ca. 40 mm long): lateral. **19.** *P. antenor*: dorsal. **20.** *P. antenor*: ventral. **21.** *Ornithoptera paradisea* Staud. (ca. 60 mm long) from Papua New Guinea: lateral. **22.** *Atrophaneura polydorus* (L.) (ca. 28 mm long) from Papua New Guinea: lateral.

pupal diapause, the adults eclosing only when new rains arrive. Preston-Mafham (1991) did not mention *A. acuminata* by name but stated that *P. antenor*'s *Aristolochia* foodplants "are well distributed throughout Madagascar in many different habitats, hence the butterfly's wide distribution within the island."

Records of Combretaceae as a troidine foodplant family have been perpetuated in the literature (e.g., Ehrlich & Raven 1964, Common & Waterhouse 1981, Watson & Whalley 1975), but these are erroneous. For example, in spite of Denso's (1943) earlier correct identification of *Aristolochia acuminata* as the larval foodplant, Viette (1955) stated that *P. antenor* utilises *Quisqualis grandidieri* of the Combretaceae. Of relevance, the phenolic acid patterns of *Aristolochia* and *Quisqualis* were compared by Das et al. (1966) and found to be different. As Weintraub (1995) pointed out, many of the early literature records have 'muddied' the pool of data on troidine foodplants. This is because many incorrect foodplants have been recorded based on erroneous determinations. My research (Parsons 1996 and unpubl. data), like that of Weintraub, has shown that troidine foodplant relations are indeed far more restricted (to Aristolochiaceae) than previous data might suggest.

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GENERAL NOTES

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A STUDY OF HYBRIDIZATION BETWEEN *COLIAS ERATE* AND *C. EURYTHEME* (PIERIDAE)

Additional key words: sex ratio, variation, phylogenetic relationships.

Hybridization among some species of *Colias* is common in nature, and many species of the genus can be hybridized under laboratory conditions (e.g., Gerould 1943, Hovanitz 1949, 1955, Remington, 1954, Ae 1959). In 1992, I had the opportunity to conduct hybridization experiments between *Colias erate* Esper and *Colias eurytheme* Boisduval. The source of the *C. eurytheme* stock was Sweet Briar College in Virginia, USA; the source of *C. erate* was Aichi Prefecture, Japan. Hybridization studies were conducted in the rearing room of the Biological Laboratory, Nanzan University, at 25°C and using fluorescent lights to create an 18 hr:6 hr light-dark regime.

Three white *C. erate* females were reared from eggs laid by a field collected, white female; the females emerged 13 May 1992. The females were placed in a screen cage (ca. 25 × 25 cm) with several field collected males of *C. eurytheme*. One of the females mated with a male almost immediately, and copulation lasted more than an hour. This female laid about 100 eggs on white clover, *Trifolium repens* L. (Fabaceae), all of which hatched. I reared the larvae of these F1 hybrids on white clover and alfalfa, *Medicago sativa* L. (Fabaceae) in the rearing room. From 10 to 23 June 1992, 25 males and 25 females of F1 adults were obtained (Fig. 1, Table 1). Concurrently, a brood of *C. eurytheme* males and females was reared from eggs from the Virginia stock on white clover and alfalfa.

Using the F1 adults, additional field collected *C. erate*, and the progeny of the Virginia stock, the following pairings were achieved: (a) three matings between F1 siblings; (b) two matings between *C. eurytheme* females and F1 males; (c) one mating between an F1 female and a *C. eurytheme* male; (d) one mating between a *C. erate* female and an F1 male; (e) one mating between an F1 female and a *C. erate* male (Table 1).

Among the mated females, one of the F1 hybrid sibling matings laid one egg; one F1 female paired with a *C. erate* male laid 7 eggs, and one *C. eurytheme* female paired with an F1 hybrid male laid 21 eggs. None of these eggs turned red, as is typical for developing *Colias* eggs, and all were presumed to be infertile. Three *C. eurytheme* females reared from eggs laid by the Virginia field collected females paired with field collected *C. erate*. One laid about 100 eggs and another laid about 40 eggs, none of which were fertile.

Colias erate has a yellow ground color and a sex-limited female white form. Japanese *C. erate* males and females have irregular yellow blotches in the marginal black band (Fig. 1), similar to female *C. eurytheme*. *Colias eurytheme* has an orange ground color and a sex-limited white form. In contrast to *C. erate*, the marginal band in male *C. eurytheme* is uniformly black, without yellow blotches (Fig. 1). The F1 males generally were intermediate in ground color (Fig. 1), however, yellow blotching in the marginal band was variable from almost absent to blotching as in *C. erate* (Fig. 2). White females of *C. erate* and *C. eurytheme* are extremely similar, as were the F1 white females (Fig. 3). Eggs, larvae, and pupae of *C. erate* and *C. eurytheme* are nearly identical, as were those of the F1 hybrids to the parental stock.

In my previous hybridization experiments, F1 hybrid males between *C. eurytheme* and *C. interior* Scudder were fertile, although the F1 sex ratio was predominantly males (26 males:1 female). The sex ratio of F1 hybrids between *C. erate* females and *C. eurytheme* males was 1:1, but they were infertile. Two *C. eurytheme* females that paired with *C. erate* males laid only infertile eggs. Although additional experiments are necessary to corroborate these results, it appears that *C. erate* from Japan and *C. eurytheme* from the United States are not closely related. There are many species of *Colias* in the world, many of which closely resemble each other morphologically. Hybridization studies such as this may be useful in identifying phylogenetic relationships among these morphologically similar species.

I wish to express my sincere gratitude to Charles L. Remington, Yale University, and


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TABLE 1. Results of hybridization attempts between *Colias erate* and *Colias eurytheme*. EU = *C. eurytheme*; Coe, ER = *C. erate*.

Female parent	Male parent	Kind of mating	Eggs laid	Eggs % fert.	F1 adults male/female	
Coe-1-7	Cou-6	Eu × Er	100	100	25	25
Coe-1-7-23	Coe-1-7-2	F1 × F1	1	0	—	—
Coe-1-7-25	Coe-1-7-8	F1 × F1	—	—	—	—
Coe-1-7-35	Coe-1-7-16	F1 × F1	—	—	—	—
Coe-1-7-46	Coe-12	F1 × Er	7	0	—	—
Coe-1-7-48	Cou-1-8	F1 × Eu	—	—	—	—
Coe-8-22	Coe-1-7-15	Er × F1	—	—	—	—
Cou-3-26	Coe-1-7-3	Eu × F1	21	0	—	—
Cou-3-44	Coe-1-7-31	Eu × F1	—	—	—	—
Cou-4-13	Coe-16	Eu × Er	—	—	—	—
Cou-4-14	Coe-17	Eu × Er	40	—	—	—
Cou-4-40-1	Coe-18	Eu × Er	100	—	—	—

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FIGS. 1–3. Adult *Colias erate*, *C. eurytheme* and their hybrids. **1,** *C. erate* female (upper left), *C. eurytheme* male (upper right), F1 hybrid (below). **2,** variation among F1 hybrids of *C. erate* × *C. eurytheme*. **3,** female white forms: *C. erate* (upper left), *C. eurytheme* (upper right), F1 hybrid (below).

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IDENTITY, RELEASE AND ESTABLISHMENT OF *CALOPTILIA* NR. *SCHINELLA* (WALSINGHAM) (GRACILLARIIDAE) ON THE ISLAND OF HAWAII FOR CONTROL OF *MYRICA FAYA* AITON (MYRICACEAE)

Additional key words: *Phyllonorycter myricae*, leaf miner.

In 1956, *Strepsicrates smithiana* Walsingham (Tortricidae) was introduced to Hawaii for the biological control of *Myrica faya* Aiton (Myricaceae), commonly known as faya or fayatree. This new association failed because *S. smithiana* established on *Myrica cerifera* L. (Julien 1992) solely at low elevations (150 m) in Hawaii. *Myrica cerifera* is the host of *S. smithiana* in its native range of Florida and Georgia. Although *S. smithiana* was capable of growth and reproduction on potted *M. faya* and *M. cerifera* at higher elevations (1200 m), it did not become established on *M. faya*.

In 1991, *Caloptilia* nr. *schinella* (Walsingham) (Gracillariidae) was first released on the island of Hawaii for the biological control of *M. faya*. This is the first agent to become established on *M. faya*, although faya has been the target of a biological control program in Hawaii since the 1950s (Davis & Krauss 1962). *Caloptilia* nr. *schinella* is a leaf miner in early instars but feeds externally on the tips of the youngest leaves in the later instars and produces silk, causing the tips of the leaves to roll. Pupation occurs on yet another leaf where an elliptical cocoon is formed on the lower surface. Adults have a plain forewing of about 7 mm in length. Problems with the insect's identity and the details of its release are discussed in this note.

Previous reports (Gardner et al. 1988, Markin 1991, Markin et al. 1991, Taylor & Markin 1992) and the release permit for *C.* nr. *schinella* refer to *Phyllonorycter myricae* Deschka (Gracillariidae). Confusion about the identification of *C.* nr. *schinella* was resolved with determinations by Gaden Robinson at the Natural History Museum, London, where voucher specimens have been retained. The released agent is presently referred to as *C.* nr. *schinella* because there are morphological and host differences from *C. schinella*. Our specimens are slightly larger and darker than the type specimens for *C. schinella*, which were collected on the island of Tenerife, Canary Islands, from *Schinus molle* L. (Anacardiaceae) (Walsingham 1907). *Schinus molle* is native to Brazil and is introduced to the Canaries. True *C. schinella* probably expanded its host range from *Pistacia atlantica* Desf. (Anacardiaceae), a native Canary Island species to the introduced *S. molle*. *Pistacia atlantica* is a recorded host of *C. schinella* in the Canary Islands, and other species of *Caloptilia* Hübner are also known to use *Pistacia* L. (Klimesch 1970). The agent introduced to Hawaii, *C.* nr. *schinella*, originates from Madeira and the Azore Islands and was collected from *M. faya* in Madeira. Although *S. molle* is also present in Madeira and the Azores, *C.* nr. *schinella* was never collected from *S. molle*. Moreover, *C.* nr. *schinella* was not found on the *M. faya* in the Canary Islands during four exploratory trips.

Host specificity tests also suggest the presence of two separate species of *Caloptilia* in the Atlantic Islands. In no-choice tests, *C.* nr. *schinella* laid 251 eggs on *S. terebinthifolius* Raddi (Anacardiaceae), but none developed beyond the larval stage, and when tested on *S. molle*, insects developed through the last larval instar and one completed development to the adult stage (Markin, unpubl. data). Unlike *C. schinella*, *Schinus* spp. do not appear to be suitable hosts for *C.* nr. *schinella*. In addition, *C.* nr. *schinella's* host, *M. faya*, is classified in the Myricaceae which is quite distantly related to the Anacardiaceae (Takhtajan 1980). Although both families are dicotyledons (Class Magnoliopsida), Myricaceae is classified in the Subclass Hamamelididae (Order Myrtales) and Anacardiaceae is classified in the Subclass Rosidae (Order Rutales).

Caloptilia nr. *schinella* was released in 1991 and 1992 at three sites in the Volcano Golf Course Subdivision and at one site in Volcano Village on the island of Hawaii, County of Hawaii. Sites in the subdivision were located at Dick Ashbaker's home at 98–2034 Popohau Place, an empty lot next to the home of Bud Doty at 99–1909 East Kaohelo Way, and

TABLE 1. Distribution of releases of 775 adult *Caloptilia* nr. *schinella* in the vicinity of the Volcano Golf Course Subdivision and Volcano Village, Hawaii, during 1991.

Site	Date	Number	Method
Bud Doty's	24 Jul	50	open
	14 Aug	60	open
	21 Aug	50	open
	26 Aug	50	open
	4 Sep	75	open
Volcano Winery	10 Sep	60	10 per sack
	12 Sep	25	open
	13 Sep	25	open
	17 Sep	50	open
	2 Oct	40	10 per sack
Dick Ashbaker's	7 May	20	tent
	20 Sep	40	tent
	16 Oct	35	open
	18 Oct	40	open
	21 Oct	40	10 per sack
	2 Nov	30	tent
Volcano Village	29 Oct	50	open

near the Volcano Winery at the intersection of Piimauna Drive and Pukiawe Circle. All three sites are located within 0.85 km of each other. The Volcano Village site was located where Road A intersects Wright Road and is approximately 3.3 km from the subdivision.

Adults were released by one of three methods: (a) into a 0.9 m × 1.2 m × 1.5 m tent enclosing a faya tree and containing a source of sugar water; (b) into sacks that enclosed one to six branches of *M. faya* and that held a supply of sugar water or lemon drops (the lemon drops were hygroscopic, dissolved slowly, and thus served as a supply of sugar and water for a week or longer; usually 10 adults were released and held in each sack for one week before the sack was removed); and (c) directly into the field. Multiple field releases of *C.* nr. *schinella* were made during 1991 on the island of Hawaii (Table 1). On 7 May, 20 adults were released into a tent at Dick Ashbaker's home. Generation time averages two months throughout the year (Markin, unpubl. data). On 24 July, 50 adults were removed from the tent and released at the lot next to Bud Doty's. This first field release also included more than 50 mature pupae and more than 300 larvae. Between 7 May and 2 November 1991, a total of 775 adults was released at the four locations with 685 released outside of the tent. An additional 30, 100, and 50 adults were added to the tent on 14 May, 21 May, and 1 June 1992, respectively. The final release was made in late June 1992 when the tent was removed and an unknown number of adults released.

Surveys of the Volcano Golf Course Subdivision between November 1991 and September 1992 located only a few larval mines and rolled tips in the field, and all were attacked by unknown natural enemies. Approximately 20 faya trees were surveyed in December 1992 near Dick Ashbaker's home and each had one or more live larvae per plant. Nearly all fayatrees located among the three release sites in the subdivision were also attacked by at least one larva. By November 1994, *C.* nr. *schinella* had established at locations up to 3 km from the release sites. As of November 1995, insects were present and reproducing in the field although their impact on faya trees appeared to be negligible.

We are conducting host specificity tests on the true *P. myricae*, described by Deschka (1976), within our quarantine facility in Hawaii Volcanoes National Park. So far, studies indicate that it is specific to *M. faya* and thus is a probable candidate for release. In contrast to *C.* nr. *schinella*, *P. myricae* is a leaf miner throughout its entire larval stage, and pupates within the mines of a leaf. Adults of *P. myricae* have forewings with white trans-

verse bars outlined in black and are only 4 mm in length. Neither agent is expected to effect complete control of *M. faya* because of faya's exceptionally invasive traits such as its ability to fix nitrogen, rapid growth rate, and high rate of seed production (Vitousek & Walker 1989).

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SEXUAL DIMORPHISM IN THE COCOON COLOR OF *BOMBYX MORI* (BOMBYCIDAE)

Additional key words: pupal color, voltinism.

The mulberry silkworm, *Bombyx mori* L., is one of the most commercially exploited lepidopteran species. Hybrids between commercial silkworm strains are reared to produce

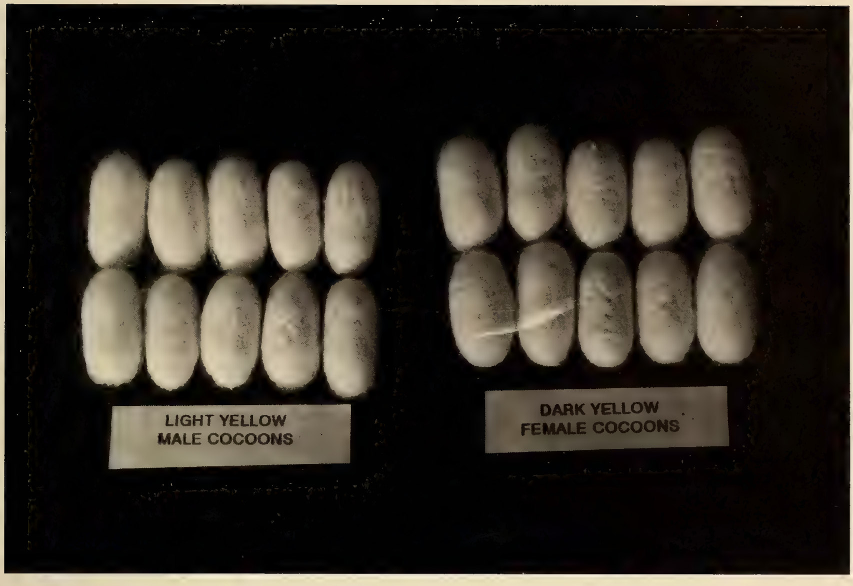

FIG. 1. Sexual dimorphism in cocoon color in *Bombyx mori*.

cocoons for raw silk production. In the production of hybrids, sex separation is necessary to prevent free mating between siblings. In the silkworm industry in India, sex separation is based on the imaginal spot on the lower segment of pupae, which provides reasonably reliable determinations but requires considerable labor (silkworm larvae have Herold's imaginal bud in males and Ishiwada's gland in females on the ventral side of the 8th and 9th abdominal segments; similar visible external characters are known in Saturniidae; see Miller et al. 1977, Miller & Machotka 1980). Pupal sexing also requires cutting open cocoons to confirm sex. In the preparation of silkworm hybrids, this method of sex separation becomes expensive when reciprocal crosses are not desired.

Several studies have been conducted on sex determination in parental races at different developmental stages in silkworms (Tazima 1978a, 1978b, Abadzhieva & Tanev 1987). Sengupta (1968) reported sex-limited characters of larval markings in a Russian silkworm race. Krishnaswami et al. (1981) observed sexual dimorphism in cocoon color in Hosa Mysore, a multivoltine silkworm race. Nagaraj and Rao (1987) succeeded in introducing sex-limited cocoon color into bivoltine silkworm races CC1 and NB4D2. However, these characters could not be commercially exploited owing to the low survivorship and stability in these races.

In the present study, we attempted to fix a breeding line from a back cross of (Mysore local × N4) × Mysore Local with sexual dimorphism in cocoon color to facilitate the process of hybrid silkworm seed production in commercial grainages with minimal wastage. Segregation of lines was made after the F3 generation. In one of the sub-lines cocoon color was found to exhibit sexual dimorphism. Studies of the sexual dimorphism began with random cocoon sampling from five batches. Light yellow and dark yellow colored cocoons were separated visually into groups. These cocoons were then cut open and sexed on the basis of pupal markings. This attempt to classify coccons was repeated four times.

In an isolated sub-line from the three way cross of (Mysore local × N4) × Mysore Local, sexual dimorphism in cocoon color was observed in the F12 generation (Fig. 1; male cocoons are light yellow in color, whereas female cocoons are dark yellow). In visually selected light yellow cocoons 96.5% were male and in dark yellow cocoons 92.5% were fe-

TABLE 1. Results of attempts to segregate *Bombyx mori* cocoons by sex using cocoon color.

Cocoon Color	Sample Size	Replications	Percent Male	Percent Female
light yellow	400	4	96.5 ± 4.7	3.5 ± 4.7
dark yellow	400	4	7.5 ± 9.6	92.5 ± 9.6

male (Table 1). The female cocoons were more elongate, less flossy and slightly larger than the male cocoons. Slightly oval, spindle-shaped cocoons were common in both sexes.

Tazima (1978a) has explained the phenomenon of difference in cocoon color between sexes and reported that cocoon color in most of the colored cocoon producing silkworm races is directly related to hemolymph color, except in some European races where the expression of cocoon color is influenced by an inhibitor gene. The presence of the yellow blood gene (Y) in silkworms is responsible for yellow color in cocoons. The allele +C inhibits transmission of pigments into any part of the middle silk gland, resulting in production of white cocoons in some silkworm genotypes. Presence of Y and +C alleles in tandem is stated to be responsible for intermediate color in cocoons and polymorphism in hemolymph color (Tazima 1978a; Ford 1975 reported that hemolymph color is always darker in females than in males of *Choristoneura pinus* (Tortricidae)).

It is interesting to note that the colored cocoon producing races of *Bombyx mori* in India, such as Nistari (golden yellow) and Mysore Local (greenish yellow), do not exhibit clear sexual dimorphism in cocoon color. However, use of these in the formation of new races through hybridization resulted in sexual dimorphism in the isolated sub-lines (Krishnaswamy et al. 1981, Nagaraj & Rao 1987, Singh et al. 1992). Similarly, in the present study, two parental races (Mysore Local multivoltine race with greenish yellow cocoon, and N4 bivoltine race with white cocoon) were combined in a three way cross to obtain a breeding line with sexual dimorphism in cocoon color. The relative importance of genetic and environmental factors in the expression of sexual dimorphism in cocoon color could not be determined in the present study. Further work is ongoing to obtain detailed information on sexual dimorphism and its relation to climatic and other ecological conditions.

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BOOK REVIEWS

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THE EMPEROR MOTHS OF NAMIBIA, by Rolf Oberprieler. 1995. Published by Ecoguild Publishers, P. O. Box 178, Hartbeespoort 0216, South Africa, in collaboration with the Namibian Scientific Society and the Lepidopterists' Society of Southern Africa. ix + 91 pages, 84 color photographs on 30 plates, one map. Hard cover, dustjacket, glossy paper, 18 × 24 cm, ISBN-0-9583889-2-X. Available from Ecoguild Publishers (FAX 1211-591506) for US $48 (postpaid, surface rate).

Virtually all books and monographs published on African saturniids have been out-of-print for many years. Saturniidae enthusiasts must seek the works by Pierre-Claude Rougeot or Eliot Pinhey on dealers' lists of used books, and, for the less available ones, they must try to find those in a regional library. Now, a nice book depicting most of the genera of African saturniids in color is again available.

The author, Rolf Oberprieler, is currently a professional entomologist at the Plant Protection Research Institute in Pretoria, but before that he was for many years a resident of Namibia (formerly Southwest Africa). Oberprieler has given us an outstanding treatment of the Saturniidae of Namibia by way of his intensive and longtime efforts as observer in the field, rearer in the lab, photographer, and finally as writer. In the Preface he acknowledges that many gaps remain in our knowledge of Namibian saturniids, but that his book is intended to summarize what is already known (including his own unpublished data) and to stimulate additional research by others. The name for the group that Oberprieler uses, namely "emperor moths," seems to follow the tradition of Pinhey who coined many common names. This appears to be based on the fact that the only saturniid found in Britain is called the emperor (*Saturnia pavonia*), and Pinhey was an Englishman. I regret that this group name has taken hold for African species, because the name "giant silk moths" seems to be well accepted in other parts of the world, except Australia, where, perhaps predictably, saturniids are also called emperor moths.

Oberprieler is a leading expert on Saturniidae. He classifies the genera *Ludia, Goodia,* and *Vegetia* in the tribe Ludiini of the subfamily Saturniinae, instead of the traditional arrangement under a subfamily Ludiinae. Well-known species like *zambesina* and *belina* (the mopane worm widely eaten by African peoples) he places in the genus *Imbrasia*, treating *Gonimbrasia* as a synonym. I concur with these taxonomic decisions. Adults of several of the lesser-known species have not heretofore been illustrated, and the larvae of many species are shown and described for the first time. Based on his knowledge of the Saturniidae of the regions bordering Namibia and their habitat requirements, Oberprieler is able to speculate that *Eochroa trimenii, Vegetia ducalis,* and *Aurivillius aratus* probably also fly in Namibia, and thus includes them in his book. Color photographs of mature larvae of several species in the tribe Bunaeini bear a striking resemblance to larvae of the neotropical subfamily Ceratocampinae (also Saturniidae). Both groups feed on small-leafed legumes like acacias and mimosas, so we may assume that this convergence of larval appearance of unrelated groups evolved to provide crypsis on the foodplants. Larvae of both groups have thick "thorns" dorsally, silver flecks laterally, and often red and yellow markings.

Although Namibia is a comparatively large country, its fauna of Saturniidae, totalling only about 28 species, must be considered as impoverished considering the large number of saturniids known from sub-Saharan Africa. Many more species fly in the moist regions of Zaire, Nigeria, and Kenya, for example, than in arid Namibia. The author discusses faunistics and ecology in introductory chapters. He also provides chapters on biology (life histories), foodplants, collection and preservation, and the historical work by earlier entomologists that led to the discovery of the various species. These discussions are instructive to both beginning and advanced lepidopterists. Concern for habitat conservation also turns up in the text occasionally. The text for each species includes sections on distribution, foodplants, and diagnosis and variation.

The book is an excellent combination of color photographs and narrative to serve as a reference for the advanced Saturniidae specialist and as an introduction to African Sat-

urniidae for the beginner. It is a well-organized work, apparently free of misspellings and typographical errors. The value of the book to readers in Africa is indisputable. However, I expect that many copies will be sold outside of Africa, because this group is unquestionably the most widely collected and reared of any moth family.

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SATURNIIDAE MUNDI: SATURNIID MOTHS OF THE WORLD, PART 1, by Bernard D'Abrera. 1995. Published by Automeris Press, Sportplatzweg 5, D-75210 Keltern, Germany, in association with Hill House, Melbourne & London. 177 pages, 76 color plates. Hard cover, 26 × 35 cm, dustjacket, ISBN-3-931374-01-7, £195 (about $300 US).

This is the first of three volumes proposed to cover the Saturniidae of the world. It includes all of the Arsenurinae, Ceratocampinae, most of the Hemileucinae (including *Automeris* and *Hemileuca*) i.e., groups all confined to the New World, plus the Palaearctic Agliinae. The stunning color photographs show all species life-size. Looking at one of the color plates is exactly like looking into a case with real specimens—there is absolutely no room for improvement on the illustrations. Upon receiving this book, I felt as if I had acquired a huge collection of hundreds of real specimens for me to use and show. It is books such as these that stimulate young people to become lepidopterists. If someone wants to become familiar quickly with the diversity of this moth family, *Saturniidae Mundi* will serve that purpose better than anything else.

The introductory text is largely a philosophical discussion, which is interesting and held my attention. To some scientific-minded readers who rarely or never expose themselves to writings by philosophers, it may be boring or even threatening, but it does not detract from the utility of the book. D'Abrera points out that his book is intended as a pictorial catalog to the Saturniidae collection at the Natural History Museum (BMNH) in London, not as a complete treatment of the family. Of course, using that particular collection ensures that the coverage will be close to complete. The author is also accepting loans from lepidopterists in other countries of specimens or photographs of species missing from the BMNH collection, some of which appear in the last two plates of Part 1.

D'Abrera has a nice historical appreciation of early literature and workers on Saturniidae. Photographic portraits of several Saturniidae specialists are shown at the beginning. He reproduces for us two of Jacob Hübner's color plates from two centuries ago. As a taxonomist, I find the citations to original descriptions of all species covered to be a very useful aspect of the book. Although the Cercophaninae and Oxyteninae are now considered by most to be in the Saturniidae, unfortunately I do not expect that they will be included in *Saturniidae Mundi*.

Since I do not work with butterflies, I have been largely unaware of the monumental works that D'Abrera has given us in the last quarter century and of the criticisms of those books. So I did some checking, both on the telephone and by reading reviews in journals, including this one. Although many do appreciate and value D'Abrera's work, I am frankly disturbed that the invalid, irrelevant, and even malicious criticisms outweigh the valid and constructive criticisms. Some examples follow.

1. "There are some species missing." I addressed this above.
2. "Edges of wings of some specimens run into the binding of the book." At least D'Abrera shows us the whole insect. Many works show us a lepidopteran body with only the right or left wings; we can only assume such specimens fly in tight circles. Incidentally, this problem has been corrected in his recent books, including this one.
3. "There are no range maps." This borders on the ridiculous. If I cannot even draw the distributional limits of the "well-known" saturniid *Antheraea polyphemus* in Canada,

Mexico, and the Great Basin, then how can D'Abrera be expected to do it for hundreds of tropical insects? I believe that a map showing a range that is greater or lesser than the real one is worse than no map at all, as it often will be misleading.

4. "The books are too expensive." Given the limited sales and high production costs for books of this type, can we expect to pay much less for a book with a large number of top-quality color plates and high-quality binding and printing? Should D'Abrera simply not produce the books because many will not be able to buy them? I cannot afford to buy a Greek island or even a yacht to get me there, but I never grumble about it. Some of the Seitz volumes in my museum's library have a price of £22 written in them, and they now would sell for hundreds. Perhaps fifty years from now people will say "It used to be possible to buy D'Abrera's books for just $300 each!" (Investors, are you listening?).
5. "Some of the species shown are misidentified." Considering that saturniid taxonomists have worked intensively in recent years in the BMNH collection, was it not reasonable for D'Abrera to assume that the specimens were correctly identified and arranged? Where does the blame really belong on this point?

As I said above, some of the other criticisms are valid. I would agree that some errors of names on the wrong illustration could be avoided by more careful checking of galley proofs. With the help of Kirby Wolfe, I am able to point out the following errors or suggestions for improvement:

1. Pages 102–103: there is no mention of the yellow male form of *Lonomia electrae*, so someone with such a specimen would likely misidentify it as *L. achelous* using this book.
2. Pages 120–121: the male figured as "*Automeris* sp." is *A. tridens*, better though wrongly known as *A. rubrescens*.
3. Pages 160–161: a specimen of *Paradirphia winifredae* is misidentified as *P. semirosea*. The latter is more widespread, yet not shown in this book.
4. Page 162: *Rhodirphia carminata* does not occur in Mexico, despite what Draudt (*in* Seitz) wrote.
5. Pages 166–167: the designer transposed seven names onto the wrong figures. *Paradirphia valverdei* is mislabeled as *Automeris peigleri*; *Paradirphia winifredae* is mislabeled as *Automeris stacieae*; *Automeris peigleri* is mislabeled as *A. ahuizotli*; *Leucanella hosmera* is mislabeled as *P. valverdei; Automeris stacieae* is mislabeled as *Paradirphia manes*; *Paradirphia manes* is mislabeled as *P. winifredae*; *Automeris ahuizotli* is mislabeled as *Leucanella hosmera*.

An errata sheet will easily correct all such errors. Regarding page 42, I believe that D'Abrera has done a fine piece of detective work pertaining to correct application of the name *Paradaemonia castanea*, and I agree with his conclusion. He clearly does not blindly accept all other taxonomic work.

If my defense of D'Abrera and his work enrages his critics, they should consider that *some* of their complaints irritated me and presumably others. I suspect that D'Abrera's worst critics buy and routinely use his books. By offering some invalid criticisms, they discredit themselves to the point that others do not take their valid criticisms seriously. I have on occasion published sarcastic and unkind reviews of books, but I feel no justification for doing so here. It is easy for the critic to tear apart in a few minutes what someone else took many months to produce.

D'Abrera's new book supports my claim that the Saturniidae are the most spectacular and popular of all moths. In spite of criticisms from me and others, the work is beautiful and extremely useful. We have some of the other volumes of his works in my museum. I routinely pull *Sphingidae Mundi* (1986) off the shelf to check something. I anticipate using and enjoying *Saturniidae Mundi* for many years to come. Despite the high cost, I highly recommend this book for museums, universities, and individuals.

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(new names in **boldface**)

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NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, General Notes, Technical Comments, Book Reviews, Obituaries, Feature Photographs, and Cover Illustrations. Obituaries must be authorized by the President of the Society. Requirements for Feature Photographs and Cover Illustrations are stated on page 111 in Volume 44(2). *Journal* submissions should be sent to the editor at the above address. Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, Phil Schappert, Dept. Biology, York University, 4700 Keele Street, N. York, Ontario M3J 1P3, CANADA. Requests to review books for the *Journal* and book review manuscripts should be sent to Boyce A. Drummond, Natural Perspectives, 1762 Upper Twin Rock Road, Florissant, CO 80816-9256. *Journal* contributors should submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded. Authors are expected to provide a diskette copy of the *final accepted* manuscript in a standard PC or Macintosh-based word processing format.

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——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

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